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Vol. 57 SEPTEMBER, 1945 No. 3

The Wilson Bulletin

Published by the

Wilson Ornithological Club

at

Ann Arbor, Michigan

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THE WILSON BULLETIN

the official organ of the Wilson Ornithological Club, is published quarterly, in March, June, September, and December, at Ann Arbor, Michigan. In the United States the subscription price is $2.00 a year. Single copies, 50 cents. Outside of the United States the rate is $2.25. Single copies, 60 cents. Subscriptions should be sent to the Treasurer. Most back issues of the *Bulletin* are available at 50 cents each and may be ordered from the Editor.

All articles and communications for publication, books and publications for review, exchanges, and claims for lost or undelivered copies of the magazine, should be addressed to the Editor.

The current issue of *The Wilson Bulletin* is printed by the Ann Arbor Press, Ann Arbor, Michigan. Entered as second class matter July 13, 1916, at Ann Arbor, Michigan, under the Act of March 3, 1879.

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Founded December 3, 1888. Named after Alexander Wilson, the first American ornithologist. The officers for the current year are:

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PLATE 11

PRAIRIE WARBLER
(Dendroica discolor)

Adult, at nest with young. Lovells, Michigan, June 19, 1944.
Photographed by Bernard Baker.

UNIV. OF MICH.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Club

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NESTING BEHAVIOR OF WOOD WARBLERS

BY S. CHARLES KENDEIGH

THE following paper is based on a study of the nesting behavior of warblers made during the summers of 1942 to 1944 inclusive on the Edmund Niles Huyck Preserve, Rensselaerville, New York. This 500-acre preserve is about 30 miles southwest of Albany, on the Helderberg Plateau on the north side of the Catskill Mountains. The observations extended each year from the first week of June until the last week of July. Seventeen species of warblers were recorded during the three summers, probably all of them breeding, but worthwhile notes were obtained on only the 12, more common, species treated in this paper. The study of several species proved difficult because the movements of the birds in the dense foliage could often be followed only by sound, and the finding of their nests was usually accidental. No attempt at monographic treatment is made here, but the fragments of life history on the various species have been brought together at the end of the paper into a composite pattern of nesting behavior.

This area is in the ecotone or transition between the deciduous forest biome and the coniferous evergreen forest biome. Hemlock, beech, sugar maple, and yellow and white birches are the dominant species. White pine is present but of minor importance. Breeding-bird censuses were taken each year in shrubby fields, in a hemlock-beech forest, and in a forest composed chiefly of deciduous trees. The most time was spent with the birds in a 21-acre hemlock-beech community. This predominantly evergreen forest is not virgin, but some of the large hemlocks are 200 years old and 75 feet in height. The forest floor is covered with a mat of dry brown hemlock needles overlaid in most places with leaves of beech and yellow birch. There is not a great amount of undergrowth nor many herbs, but here and there the young second growth forms a dense stand. Figure 1 shows the degree of mixture of hemlock and beech, as well as the relative size of the trees.

On each survey of this community, the location of every bird observed was marked on a map of the area. After a few such surveys the approximation of marks permitted drawing of territorial boundaries as shown in Figures 1 and 2. This, together with peculiarities of song,

made it possible to recognize individuals, although with less certainty than if the birds could have been color-banded. The boundaries of the territories as drawn and the measurements given for them are only approximate, and they may generally be too small. They were most accurately determined in 1942, when the greatest amount of time was spent in this area. It is entirely possible that more time spent in observing the birds in 1943 and 1944 would have shown that some of the territories were larger than they appear on the map. These territories were simultaneously occupied, although not continuously so, during the breeding season. For the Oven-bird and Magnolia Warbler, which have two breeding periods, the territories as mapped include the total area occupied for both broods, since there seemed to be very little change in the boundaries. A very few males, chiefly Oven-birds, were present only during the latter part of the season. Birds whose territorial boundaries were not determined are indicated on the maps by numbers in parentheses placed at the approximate center of the area of their activities.

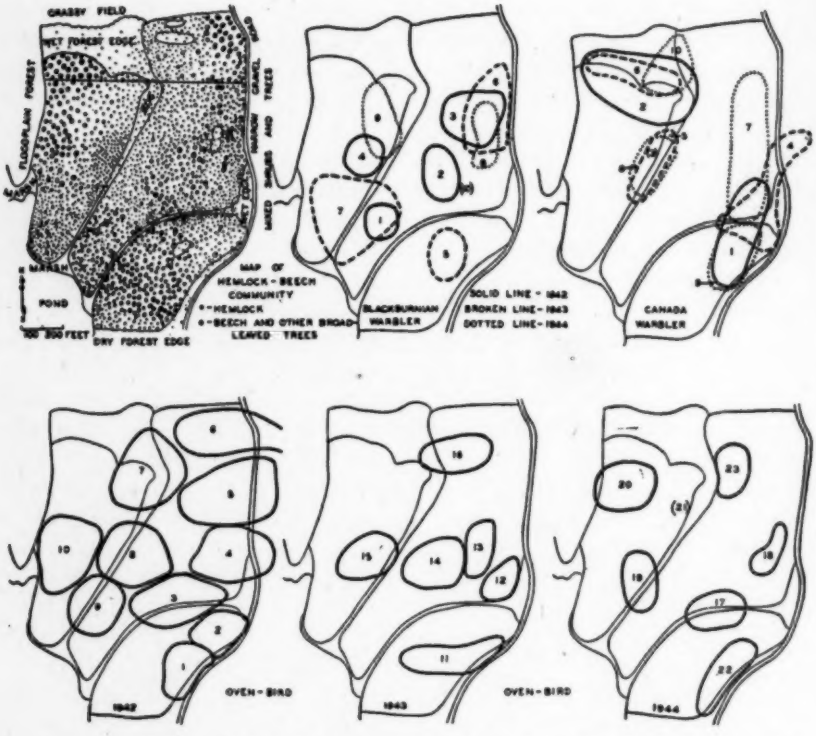

Figure 1. Map of hemlock-beech community and territories of warblers studied. Numbers in parentheses represent territories the exact boundaries of which were not determined.

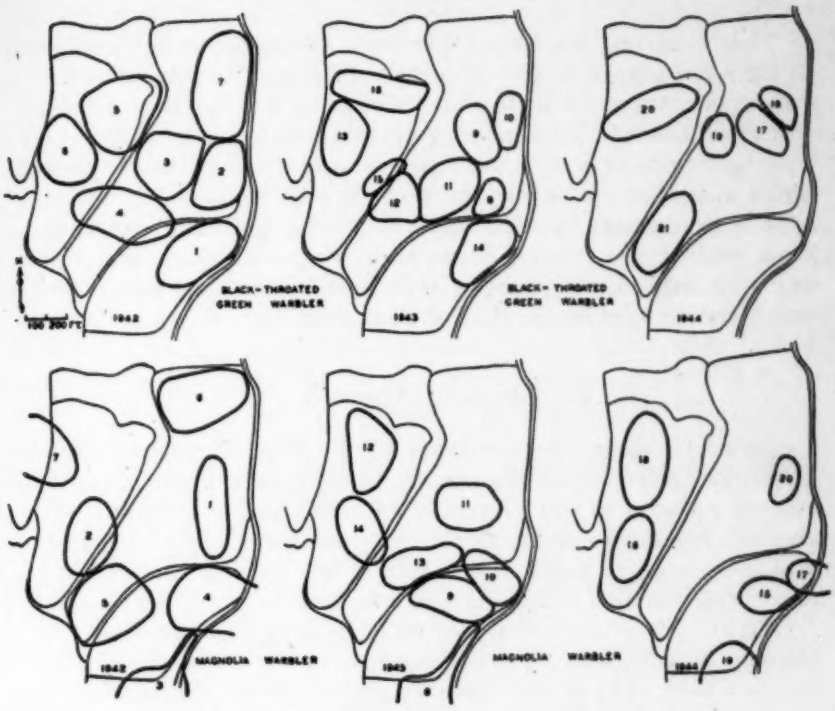

Figure 2. Territories of warblers in a hemlock-beech community.

Black and White Warbler

Male Black and White Warblers (*Mniotilta varia*) sing incessantly until mated. They seek exposed singing posts at or near the tops of isolated trees in shrubby fields, and perch crosswise on a branch. One song was syllabized *zii zii zii ziii-eee ziii-eee ziii-eee,* the first three notes being single, the last three double. A variation was a series of about eight short *zii* notes followed by a trill. About the middle of June, when nesting is well along, these warblers become almost entirely quiet and are easily overlooked. At a nest with 5 young about 4 days old, the young were fed twice by the male, 3 times by the female during 2 hours afternoon observation. This seems a very slow rate of feeding, yet the young successfully left the nest on June 29, when 8 or 9 days old.

On June 15, a pair of Black and White Warblers were much concerned over a young Oven-bird not long out of the nest and apparently separated from its parents. The young bird was calling loudly for food. The Black and White Warblers were apparently caring for it, although they were not actually observed to feed it until 3 days later.

Nashville Warbler

Male Nashville Warblers (*Vermivora ruficapilla*) sang from posts on the forest-edge at heights from 15 to 30 feet. The song consisted of a series of notes of the same pitch followed by a descending trill, probably a variation of the second song described by Saunders (1935: 182). The singing posts are often inconspicuous and the birds difficult to find. Males were observed on two occasions silently chasing other birds for some little distance in what appeared to be territorial competition. When excited, the females flutter their wings. Although adults were seen with food for the young in their bills, no nest was found. Fledglings were observed by the third week in June.

Magnolia Warbler

Figure 2 shows the territories of 20 male Magnolia Warblers (*Dendroica magnolia*) during the first breeding period. Fifteen of these average 1.8 acres in size. Territory 20, which was in a dense shrubby area and measured only about 0.6 acre, was the smallest. Territory 4 was quite large, probably 3 to 4 acres if one includes the area in the pine-spruce planting across the road where the nest was later built.

Territory is established and defended by song, plumage display, and chasing. Singing posts are most frequently on the outer edge of a hemlock and from 10 to 45 feet above the ground. When vigorous, the song may be repeated 10 times a minute. The song commonly given for territory and mate has been frequently described by others, e.g. *wee-o, wee-o, wee-chy* (Stanwood, 1910:384); there are, however, many variations. Another song for the same purpose, *ta hé ta heéch a*, may be the same as the second common song described by Brewster (Griscom, 1938:575). A song given during the progress of nesting or when the bird is patrolling a well-established territory consists of a series of notes (usually four), all of the same pitch: *mae mae mae mae*, or *cheel cheel cheel cheel*. The male Magnolia sings persistently day after day but often in a desultory manner. However, when a new male comes in to establish a territory or a male attempts to expand his territory, singing may be very vigorous and stimulate the males of this species over the entire woods to join in and assert their claims. Such responses show how closely knit and balanced a society these birds form when there are several territories in a comparatively small area.

When another bird of the same species intrudes in spite of the warning song, the male in possession of the territory flits nervously but silently around from branch to branch with tail spread, showing its white markings. Occasionally the resident male will fly out at the other male with tail and wings spread in display and then circle back without giving real chase. On several occasions when more vigorous resistance was required, the male suddenly stopped singing (sometimes uttering a

few chirps) and gave full chase to the intruder without any attempt at plumage display. Once a male chased two male Black-throated Green Warblers that were squabbling near-by.

During the mating period, when a female enters the territory, the male stops singing and begins a display which is more complete than that used in territorial defense. With spread tail and wings the male follows the female through the trees from branch to branch, or sometimes flies directly at her. Nice (1926:193) has described a *kree-ee kree-ee* note given by the male when "courting" his mate late in the nesting period.

When nervously excited, the female also displays, at least to the extent of flitting her tail and exposing its markings. There was no evidence that the female recognized the limits of the territory that the male established. When leaving the nest during the incubation period she sometimes went well outside the male's domain. But she did resent intrusion in the immediate vicinity of her nest. Twice during the incubation period a female drove off male Magnolia Warblers that had been attracted by her scolding of me.

The behavior of the adults was watched at only one nest, and this for only 2.5 hours two days before, and for 2 hours shortly after, the eggs hatched (both times in mid-morning). During the first observation, the female incubated steadily for 2 hours with hardly a restless movement, left for 20 minutes and then returned for another attentive period. The male did not come near. During the second observation, the female brooded the newly hatched young for 20 minutes after being away 13 minutes, left for 4 minutes, brooded again for 24 minutes, was gone for 5 minutes, then back to brood for 12 minutes, when her stay was interrupted by the male's appearance. During the next half-hour the young were fed twice by the male, 3 times by the female, and the female brooded for 2 periods of respectively 13 and 10 minutes. Observations of Stanwood (1910:386), Mousley (1924:280), and Nice (1926:196) indicate that the incubation period lasts about 12 days and that the young leave the nest 8 or 9 days after hatching.

The Magnolia Warbler begins nesting rather early, and fledglings were found in 1942 on June 15; in 1943, on June 24. Second broods are regularly attempted, and the males sing energetically during the latter part of June while re-establishing their territories and acquiring mates. Singing continues until the end of July.

Black-throated Blue Warbler

One male Black-throated Blue Warbler (*Dendroica caerulescens*) was in the northeastern corner of the hemlock-beech study-area at the beginning of June, 1942; on June 18 a second male intruded on the area of the first male without being molested but later became estab-

lished with a female just to the south. In this species the males seem more tolerant of each other than in most species of warblers. Once, for example, a male was observed singing and feeding 15 to 20 feet up in a beech when another male, likewise singing, was 30 feet up in the same or in an adjacent tree; the two birds appeared to pay no attention to each other. It was common to find two males thus singing near each other, and birds often shifted around in an apparently aimless manner. Males were frequently observed far from their usual posts (often as much as 500 or 600 feet); they sang as they gradually worked their way back. Probably with this species, as with some other warblers, the concept of "home range" should be retained, since it is doubtful whether the entire area, often several acres, over which the birds wandered was regularly used and defended. Some competitive singing between males and chasing of one male by another was observed, but the actual portion of the home range that was defended as territory was not satisfactorily measured.

There are two common and easily recognized songs in this species, and each song has variations. Both songs may occasionally be given by the same bird, but usually one or the other song predominates with any one male. One song is given slowly and has a harsh quality; *wheer wheer wheeee* (Chapman, 1907:137). Usually there are three *wheer*'s, but one male gave only one. The other song is faster, and the notes are sharper: *zee zee zee zee zeeeee*. Both songs end with an upward slur that involves all of the last note and sometimes with the second song includes several of the preliminary *zee* notes.

On June 10, 1943, a male and female were observed feeding together, the female energetically, the male half-heartedly. The male appeared excited but sang little. Once he flew to the limb beside the female, partially spread his wings in display, then left. Very soon he sang softly once, then flew to the female, uttered several chattering notes, displayed his wings, chased her two or three feet into denser foliage, and apparently copulated with her. He continued his display, without singing, and finally chased the female some distance away. Four days later, another male, considerably outside his usual area, was observed chasing a female. He was very excited; he did not sing but uttered the same peculiar chattering notes. Again copulation apparently followed. These chattering notes are the same as the alarm notes described by Harding (1931:517) as a series of *thck's*. On July 10, a pair was observed feeding young near this location.

In 1943, the behavior of birds at a nest was watched from the time the nest was begun, on June 29, until the young left on July 25. The nest was in an upright fork of a purple-flowered raspberry in a deciduous forest and was only one foot above the ground. During 36 minutes of observation on the first day, the female did all the nest-building, making 21 visits; the male did not appear. The female once chased away a male Chestnut-sided Warbler that came too near the nest. Because of

the lateness in the season this may have been a second attempt at nesting. Elsewhere in the woods on this same morning, another pair of adults was observed carrying food.

On July 1, the nest was fully built but empty. During 71 minutes of observation, the female came once and sat in the nest for 7 minutes, squirming and kicking around part of the time. The male came twice when the female was absent and sang near-by, but did not approach the nest itself. Presumably the first egg was laid the next day since there were two in the nest at 8:16 A.M., (E.S.T.), July 3. During 94 minutes observation on that day, the male was absent, and the female came to the nest once, sitting quietly on the eggs for 20 minutes.

On July 5, there were 4 eggs in the nest, and incubation was well under way. During 5.3 hours of observations made at various times of day, and spaced at 3- and 4-day intervals throughout the incubation period, the attentive periods averaged 28 minutes in duration, varying between 22 and 40+ minutes, and the inattentive periods averaged 9 minutes, varying between 5 and 15 minutes. The male was not recorded a single time during this period either around the nest or singing near-by. This does not agree with observations by Harding (1931:513, 516), who observed the male taking part in nest-building and feeding the female while she incubated.

Two young had hatched by 12:50 P.M. on July 16; at 8:00 A.M. the next morning the third young had appeared, and at 4:45 P.M. the fourth was out of the shell (an incubation period of 12 days). One young had disappeared by July 23, but the other three had matured sufficiently to leave the nest early in the morning on July 26. Thus their nestling life was 9 and 10 days long.

During the period of hatching on July 16 when there were 2 young and 2 eggs in the nest, the attentive periods of the female were 11, 25, and 10.5 minutes in length and the inattentive periods, 3, 8, 2.5, and 6 minutes, indicating a shortening and a greater irregularity of both periods compared with attentive and inattentive periods during incubation. During 68 minutes, the female fed the 2 young 5 times. The male was not present.

Approximately 1.7 hours were spent in observation at the nest, beginning at 9:10 A.M. on July 20, when the young were 3 and 4 days old. The female was at the nest for periods of 19, 11, and 37 minutes, although much of this time she stood on the rim and worked with her bill inside the nest. The irregularity in the length of her attentive periods was due in large part to the male's coming to the nest with food and interrupting her stay. The male fed the young 6 times, and the female fed them 3 times. The male invariably sang as he approached the nest, and this appeared to be a notice for the female to prepare to leave. The song was given softly and was often incomplete.

On July 23, when the young were 6 and 7 days old, the female brooded 13+ and 10 minutes during the 105 minutes of observation

beginning at 8:33 A.M. She fed the young 4 times and the male fed them 3 times. The male's behavior when approaching the nest alone was the same as before; twice the male and female came to the nest together. The young now had their eyes open, and the tips of their pin feathers were beginning to break open. They left the nest 3 days later. During the 3.4 hours observation on July 20 and 23, the young were fed on the average once every 13 minutes. This is in marked contrast to the average interval of 2.4 minutes recorded by Mousley (1924:274).

Black-throated Green Warbler

Twenty-one territories of the Black-throated Green Warbler (*Dendroica virens*) averaged 1.6 acres in extent and varied from 0.6 to 2.5 acres in size (Figure 2). Territory 1 represents an unusual case since the territory was occupied consistently only until June 10. After that it appeared that the male had a mate with a nest across the road in a dense pine-spruce planting. On July 3 a male with the same type of song and accompanied by young out of the nest was in the original territory. Territory 15, a very small one, was also only temporarily occupied.

Territories are especially important with this species, and intrusions by other males are met with vigor. The male immediately gives chase and drives the other bird to the boundaries of his area. If the intruder remains in the vicinity, intermittent chasing may continue for several hours. There may be chipping notes given, but there is no singing nor usually any special plumage display. Once a male was observed to dart after another male and then to hover for an instant. Competitive singing sometimes occurs between males on adjacent territories when no trespass is involved. On June 28, 1943, two, or possibly three male birds were in a part of the hemlock-beech forest three or four hundred feet away from the nearest active territories. There was some chipping but no singing, although the birds seemed aware of each other's presence. This is apparently an instance of wandering by males outside of established territories, which is common in warblers although this wandering tendency is less marked in this than in some other species.

There are two main variations in the song melody of the Black-throated Green Warbler, as has been frequently noted by others. This fact, together with secondary variations in the song and the male's persistence within mapped territories, permitted recognition of pairs throughout most of the season or until they began to wander with their young. Sixteen of 27 males sang a song described by Pitelka (1940:14) as: *zrrr-zrrr-zu-zu-zwee*. Some males uttered this intermittently amidst a constant stream of low chips. The first, second, and last note are rasping in character. The second note, as given in this region, is higher than the first in pitch, not lower as Pitelka diagrammed it for birds in Michigan. This rendition is somewhat similar to the third

example of the second type of song described by Saunders (1935:191). As one moves away from a male the last note is lost to audibility first, then the first and second notes, while at a still greater distance the more metallic third and fourth notes alone can be heard. There is less variation in this song than in a second song. Eleven males had a song described *zee zee zee zee zu zwee* by Pitelka. In this song the fifth note (*zu*) was on a lower pitch than the others and was occasionally doubled; some males uttered three or five instead of four preliminary notes. In both the *zrrr* and the *zee* types of song the last note is slurred upward. The song of any one individual was almost exclusively one or the other type (or a variation of one type). In 1942, there were only one or two doubtful instances of a male uttering both types of song; in 1943, at least 3 males sang both types of song rather frequently. Singing persisted even after the young left the nest or until mid-July.

Two pairs in 1942 had young out of the nest on June 23, another pair on July 3, and others soon after. In 1943, such families were not seen in the hemlock-beech forest. Perhaps they were there, though not seen by the observer, but since red squirrels were unusually abundant that year, and the population of Black-throated Green Warblers was considerably reduced in 1944, there is reason to think that much of the nesting was unsuccessful. This species apparently raised only one brood in a season.

During 2.5 hours of nest observation divided between 2 afternoons the young were fed 6 times by the male and 7 times by the female with the sex doing one feeding undetermined. This was at the rate of once every 11 minutes. Part of the female's time, however, was occupied with brooding.

Blackburnian Warbler

Since the Blackburnian Warbler (*Dendroica fusca*) frequents the highest stratum of the tree tops, observations of this species were particularly difficult. Nine territories were marked out, mostly from the location of songs heard, and their average size was relatively small, 1.3 acres (Figure 1).

Saunders (1942:253) describes the song of these birds in southwestern New York as a series of two-note phrases followed by a trill which is commonly lower in pitch than the rest of the song: *tsita-tsita-tsita-tsita zzzzzzzzz*. At Rensselaerville the trill is more commonly a slur rising in pitch, although one unmated male, perched on a projecting dead limb high above the forest canopy, sang an elaborate song with a trill descending in pitch and ending with a final *tsee*. After a male acquires a mate and settles down, the song often consists of the initial series of double notes only. By the end of June or the first week of July, singing ceases except for occasional notes.

A nest was found on June 18, 35 feet up in a hemlock in an inaccessible location 6 feet out on a horizontal limb. Its construction was nearing completion with the lining being inserted. In 82 minutes of observation the female visited the nest 7 times. The male occasionally sang near-by and once alighted near the nest, but the female spread her wings and chased him away as if she would not tolerate his presence in the immediate vicinity. On June 21, during 15 minutes of observation, neither adult visited the nest, but a non-singing bird, possibly the female, was seen to chase a male Black-throated Green Warbler out of the territory. On June 24, incubation apparently was under way. During 53 minutes of watching in mid-afternoon, the female incubated twice (for 10 and 18 minutes), and was inattentive for 15 and 10 minutes. The male sang periodically nearby. The next morning the female, while under observation, incubated for one period of 30 minutes and was inattentive for periods of 9 and 10 minutes. The male was not seen.

Chestnut-sided Warbler

In 1940, Eugene P. Odum, then resident naturalist on the Preserve, noted the arrival of the first males of the Chestnut-sided Warbler (*Dendroica pensylvanica*) on May 14 and the first females on May 22. In 1942, the first females must have arrived about the same date since the first young being cared for out of the nest were observed on June 22. However, many females were delayed in starting to nest; in six instances signs of first mating behavior with arrival of females in the males' territories were observed, on June 5, 8, 10, 12, 12, 12. The sexes are not always easy to distinguish in the field, although the male has a darker back and a brighter crown. Only the male sings, as is true also with the other wood warblers, and the female is usually shy and retiring, keeping well down in the low bushes and briers.

The unmated male on his territory, which is typically an open shrubby field containing patches of briers, bushes, and scattered trees, spends much of his time singing from tops of bushes or from the lower branches of trees. During the early season the song may be given 5 or 6 times a minute and may be heard at any time of day. The song is of two types. In the establishment of territories and advertising for mates it is characteristically clear and loud and may be heard at some distance. Jones (1900:35) has given the best rendition of it, *te te te te we chu*, with the fifth note accented and of higher pitch. Developing gradually from this song as the season progresses is one of a different character that Saunders (1942:254) renders, *wayo wayo wayo wayo weeo weeo wayo wayo*. Commonly the last two notes are not given, and *weeo* is more nearly *wheea*. This second song is more common after incubation is well established, is not given so vigorously or sharply, and seems to indicate a lower emotional level. It serves as a signal of territorial possession rather than of competition, although two males on adjacent

territories were once observed giving this song alternately when only 30 feet apart.

Ordinarily there are several song posts habitually used by the male on his territory, and he sings successively from one, then another, until he completes the round of his possessions. Where the territories of two males lie close together, the males occasionally compete in song. On several occasions one male was seen to chase another out of his territory, once fully 200 feet. In this singing, chasing, and competition between males there is no special plumage display aside from that which occurs with the normal movements of parts of the body.

The female enters the territory quietly and inconspicuously by short flights from branch to branch through the bushes and trees. When the male sees her, he becomes silent and may dive at her or chase her from limb to limb. As his excitement grows, he makes a plumage display. This may occur as he alights near the female at the end of a dive from a high perch; it lasts only a few seconds. The tail feathers are spread, the wings extended, and crown feathers erected. The wings and tail quiver up and down. The female may display in return, though less vigorously. Doubtlessly this plumage display is mutually stimulating and leads to the emotional pitch necessary for coition. After one such dive by a male a series of chattering notes was heard, but copulation, if it occurred, could not be seen in the dense foliage. There is no singing during the display, although subsequently the male may fly excitedly around, give his first song described above, and chase other birds that normally he would not notice.

The male accompanies the female in the search for a nest-site, following her closely from tree to tree or bush to bush. There may be occasional singing, but they are mostly quiet, and they carry on some feeding. The male may slightly spread and droop his wings and partly raise his tail in a manner typical of pre-copulation behavior in other species. The female appears more intent than the male in the search for a nest-site. One nest was later found in a brier patch about 50 feet away from where a vigorous dive and plumage display by a male had been seen. However, the female looks for, and often establishes, nest-sites outside of the male's original territory. The male is somewhat attentive to the female during nest-building and egg-laying, but his enthusiasm is less sustained. He continues to sing during the incubation period, although he is quiet for long stretches of time. These quiet periods become more frequent as incubation continues.

Previous to the mating period, the male's territory, in three instances that were measured with some accuracy, covered 1.2, 1.3, 1.3 acres respectively, and two other known territories were about the same size. Another territory was estimated at 2.5 acres. During the incubation period, or during protracted pre-mating periods, the male greatly extends the area over which he roams, going well outside his previous

territorial boundaries. This was observed repeatedly and regularly with several males. They wandered from 200 to 700 feet, and covered from 2 to 12 acres, or even more. On these long excursions the male sings his *wayo wayo* song more frequently than the *te te* song, although they may both be given. This singing, however, is much less vigorous and less frequent than on the territory itself; there may be long periods of silence; or the male may not sing at all. There is no evidence that these larger areas are defended, although the desultory singing may serve to ward off intruders. It is best at present to designate this area simply as the bird's "home range" and to limit the term "territory" to that portion of the home range where singing is vigorous and regular or where there is chasing or other types of defense. The home ranges always extended into free and unoccupied areas. In no case did the home ranges of two males overlap, although this may have been because the birds were few and fairly scattered.

On June 22, 1943, a nest was found just being built at the edge of a shrubby field, in the triangular fork of a bracken fern only 2.5 feet from the ground. The female was working on the nest foundation at the time, coming to the nest with materials at about one-minute intervals. The next afternoon the nest was well formed, and the female was busy finishing the interior. She made 9 trips in the first 52 minutes of observation but was then absent for the next 38 minutes. The male sang unexcitedly and made some attempt to follow the female. Once he looked into the nest when the female was away. Another time he followed the female to the nest and displayed to her on its rim, uttering a *tsiip*. Early on June 25, the nest was practically complete, and the female apparently brought no new material, although she would sit in the nest and work at the lining. She made six visits in an hour. One visit was interrupted when she gave chase to a male Golden-winged Warbler (*Vermivora chrysoptera*) that came within a foot of the nest and again a minute later when it came within 15 feet. The male could be heard singing his *wayo wayo* song in the distance but was not seen near the nest.

The first egg was found in the nest early the next morning. During an hour's observation a male sang in the distance. The female came to the vicinity of the nest 6 times but only once went to the nest itself; then she sat on the egg for 2 minutes. Once she chased away a yearling male Redstart that came within 20 feet of the nest. The third, and last, egg was in the nest on June 28, and incubation had begun. All eggs were hatched by July 9 (an incubation period of 11 days); two of the young were so much larger than the third that they had probably hatched the day before.

Four and a half hours of observation, divided fairly evenly on the afternoons of June 28, 29, July 1, and 7, gave an average of 13 minutes for 11 attentive periods, and 8 minutes for 10 inattentive periods (ex-

cluding one long inattentive period of 23 minutes on the first day of incubation). A male could frequently be heard singing in the distance but was not observed near the nest. It appeared that the male's territory was chiefly to the north, and this nest-site was on the very edge of it or may even have been outside of it as originally established. The female almost invariably went north (in the direction of the territory) when she left the nest.

At another nest, under observation in 1942 for 8.7 hours scattered in morning and afternoon throughout the incubation period, the attentive periods averaged 21 minutes in length and the inattentive periods a little over 6 minutes. The female during incubation at this nest seemed quite independent of the male. Although the male occasionally sang near the nest, only twice in 21 times that she was observed to leave the nest did she appear to do so because stimulated by the male's presence. These departures ended attentive periods of only 11 and 16 minutes. The longest period observed was 27 minutes. The inattentive periods varied between 4 and 9 minutes.

The eggs in the 1942 nest, perhaps because of accidental jarring by the observer, did not hatch. On the day the young were found hatched in the 1943 nest, the male was back helping to feed them. In 1.4 hours of watching during the afternoon he brought food for the young 3 times and the female brought food twice. The female brooded 2 times (26 and 34 minutes) with inattentive periods of 11 and 13 minutes. On the morning of July 12 when the young were between 3 and 4 days old, the female during an hour and 26 minutes of observation brooded for one long period of 35 minutes after the preceding brooding period had been cut short at 4 minutes by the arrival of the male. It is of interest that this female's attentive periods while brooding the young were considerably longer than while incubating the eggs. On this same date the female fed the young 4 times and the male fed them 7 times, once interrupting his feeding to drive off a yearling male Redstart. The young were gone on July 16, only 7 and 8 days after hatching, and it is uncertain whether they left naturally or were taken by a predator.

Another nest was found on June 17 with young one or two days old. When first discovered, the female flushed from the nest, fluttered along the ground as if wounded, uttered scolding notes, and the male approached within a couple of feet. During an hour's observation in the afternoon, the female came to the nest 6 times (not certainly with food each time) and brooded twice for periods of 12.5 and 21 minutes, the brooding periods being interrupted or terminated when the male arrived with food. The male sang frequently and fed the young 5 or 6 times. On my return to the nest on June 24, 7 days later, the young were gone. On two or three occasions the male has been seen caring for the young out of the nest, and it is likely this duty continues to be shared by both sexes until the young become independent.

Oven-bird

Although territories for the Oven-bird (*Seiurus aurocapillus*) in the hemlock-beech study area were mapped (Figure 1) and several nests were located, little attention was paid to its behavior. Chasing, however, was frequently observed, and the "flight song" was heard several times. One performance was especially spectacular. There was a swift musical jumble of notes, apparently given at the beginning of the flight, for immediately afterwards the bird came into view, doing a loop that extended from the level of the tree tops (30 feet high) down to the ground. The bird seemed to have its wings folded close to its body and to be making a swift dive.

Apparently two broods are raised. The size of 21 territories varied from 0.25 to nearly 3 acres and averaged 1.6 acres. Song was greatly reduced after mid-July.

Louisiana Water-thrush

A single nest of the Louisiana Water-thrush (*Seiurus motacilla*) was found on June 10, but unfortunately not until the four young were 5 or 6 days old. Three days later, the young were fed 7 times in 53 minutes of observation. Apparently most of the feeding was done by the female; a male was singing in the distance a large part of the time. The young were still in the nest on June 15 when they were at least 10 days old. The exact time of their leaving was not determined.

Yellow-throat

The Yellow-throat (*Geothlypis trichas*) begins nesting early, for the first young were out of the nest by June 15 in 1942. On June 19, there was considerable commotion among the Yellow-throats inhabiting the shrubby-field study-area. There seemed to be an influx of new males, and adults with their young were roaming around on each other's territories and upsetting the normal equilibrium. It was also obvious that the males were making an effort to reestablish territories and secure mates for a second brood. There was chasing of one bird by another in wide circles and considerable singing both of the normal song and of the flight song. The excitement continued at a slightly lower level during the rest of the month and into early July when the second nestings were under way. In 1943 and 1944, this period of excitement and readjustment for second broods was again evident during the third week of June.

Although male Yellow-throats commonly sing from close to the ground or from low bushes, they mount higher under the influence of competition, even to 40 feet or more. As if this were not sufficient, they also have a song given during either a vertical flight or a horizontal one that begins with their usual song and ends with an outburst of ecstasy after which the bird flutters down to the ground or to an exposed perch. One horizontal flight song at a height of fully 100 feet was observed at

7:00 P.M. These flight songs may be heard well past the middle of July.

Territories were not mapped for this species, but in 1942, 7 pairs were fairly uniformly spaced over an area of 5 or 6 acres, which would make their territories less than an acre in size. The incubation period at one nest was 12 days long.

Canada Warbler

Male Canada Warblers (*Wilsonia canadensis*) have a clear, abruptly tumbling song (Saunders, 1935:217) that they commonly utter at a rate of 6 times per minute when advertising for a mate. Soon after a mate is secured they usually become very quiet. Since the young of one nest left on June 19, and at another nest they were nearly ready to leave on June 23, nesting must begin soon after the middle of May.

In spite of persistent singing, one male in 1942 was unable to secure a mate until the third week in June. The size of his singing area was only about 0.6 acre, but after nesting began he wandered over 2 acres, although then he was usually quiet. Another male, with a nest, roamed over 3 acres or more, an expansion of an earlier singing area. This again appears to be an example of a larger area being used after nesting has begun. With this species, however, there is some evidence that the entire larger area is vigorously defended against intruding males by scolding notes and by silent chasing. In Figure 1, the entire larger areas are mapped.

Redstart

Two male Redstarts (*Setophaga ruticilla*) in yearling plumage were regularly observed in the same thicket or patch of trees and evidently had established territories and nests. Other singing males in yearling plumage appeared to move around considerably and were apparently without mates. The majority of the males were in full adult plumage, however, and showed no wandering tendencies. In 1944, none of the estimated 10 males on the Preserve was in yearling plumage.

Adult males in this species are strongly territorial in behavior, defending their possessions by song, color displays, and chase. There is a variety of songs, a common one being: *zwee zwee zwee ze ze zump* with the fourth and fifth (*ze*) notes at higher pitch than the first three, and the last note at a lower one. Another series of notes at the same pitch resembles a song of the Black and White Warbler. Redstarts sing from perches up to 40 feet from the ground.

Chasing occurs on slight provocation and is not accompanied by singing though it may be preceded by sharp scolding notes or by a period of competitive singing. One male was seen to chase another for fully 200 feet. Redstarts were also observed to fly after Oven-birds and juvenile Hairy Woodpeckers. These chases are straight and rapid, and there is no plumage display except that which is incidental to movements of wings and tail.

A special flight maneuver has been described by Hickey (1940:255) that serves primarily as a threatening plumage display. These darting flights were observed in the present study only once or twice and only between males. In Hickey's words they consist of "short, horizontal, semi-circular flights made with stiffened wings and out-spread tails. These performances were frequently observed between males, less commonly between females and never between a male and a female where a question solely of territory was involved. . . . Low, repeated *quit quit* notes could be heard when the displays were concluded and the birds returned to their perches. As far as could be observed, these same performances seemed to serve as some part of the male's courtship of females. . . . The size of territories was usually about one acre or less. . . . Their boundaries were observed in two cases to break down on June 17, when young were being fed in the nest."

In courtship activities, a male in full adult breeding plumage may fly after a female, alight beside her, and spread his tail, showing its brilliant coloration. His wings may not always be extended, and he does not sing. He may retain the pose for several seconds before they both fly away.

Two nests were found in 1943 and one in 1944. On the mornings of June 12 and 17, 1943, during 119 minutes of observation at a nest containing eggs, the female's 10 attentive periods averaged only 9 minutes in length; 11 inattentive periods averaged only 2 minutes. The male sang nearby, and on the latter date came to the nest and flitted around it.

At the 1944 nest, 153 minutes of observation in both morning and afternoon on the second, third, seventh, and eleventh days of the incubation period covered 5 attentive periods that averaged 18 minutes and 6 inattentive periods that averaged 7.5 minutes. There was one exceptionally long inattentive period of 19 minutes. In this nest the fourth egg was laid on June 6. Since 3 of the young hatched on June 17 and the last not until June 18, it is probable that rather steady incubation began with the third egg and that the incubation period is 12 days long. The young left on June 27, which gave them only 10 days for development in the nest. In 53 minutes of observation in late morning when the young were 3 and 4 days old the female brooded 3 times for periods averaging 15 minutes, with inattentive periods averaging 4 minutes. The female's brooding was interrupted by the male bringing food. This he passed to the female who then fed the young. When the female was absent, the male fed the young directly. The male brought food 12 times, the female only once; this gives an average of once every 4 minutes for feeding the young.

There were half-grown birds in the third nest when it was found. On June 22 and 26, 94 minutes were spent watching the nest, beginning about 9:30 A.M. each day. On the first date the female brooded 3 times

for 5, 6.5, and 2 minutes, with the male coming to interrupt her each time as he brought food for the young. Her inattentive periods were 2, 1.5, and 15 minutes long. On the first day the male fed the young 5 times, the female fed them 4 times; on the second date, the male fed 6 times and chased away a female Yellow-throat and an unidentified bird; the female fed the young 4 times. When a disturbance was made near the nest, both adults came scolding and flashed their tail markings as they flitted through the branches.

Discussion and Summary

Although there is variation in details from species to species, nevertheless there is sufficient agreement to permit description of a general pattern of nesting behavior for wood warblers. The following remarks are based primarily on the original observations reported here.

Song is used for marking out and advertising a defended territory. When song is not sufficient to keep an intruder away, chasing results. There is no evidence that fighting or physical combat between males takes place, except possibly in the Oven-bird (Hann, 1937:151). Song is distinctive for each species, and variations in the song are often characteristic of different individuals. Geographic variations in song also occur, since descriptions given by different authors vary in important details. In addition to proclaiming territory, song is used to attract the female but not as a primary stimulus leading to coition. After mating is completed, singing is less enthusiastic and less frequent and there are sometimes modifications in the character of the song. During the incubation period, the singing of the male helps to maintain the territory and in some species or in some pairs has an influence in modifying the female's attentive behavior. Singing greatly decreases at the time the eggs hatch but may be renewed with vigor between a first and second brood.

Nearly all wood warblers are strikingly marked and often brightly colored, especially in the male. Nichols (1913) lists three principal functions for warbler coloration: concealment, recognition, and advertisement and display of the male. The coloration is displayed to advantage by spreading the tail, extending the wing, and erecting feathers on the crown or elsewhere on the body. A partial display may be given when the male is excited by an intruding bird, but it reaches a climax when the male is exciting a female toward coition. This display takes the place of a mating song, although notes of excitement may be uttered preceding coition. In the Redstart, and to a lesser extent in Magnolia and Black-throated Green Warblers, a darting semi-circular flight with full display of color has developed for intimidation of intruders in territorial defense. Coloration doubtlessly also serves for recognition of species and sex by the birds themselves.

In addition to the defended territory, some warblers (Chestnut-sided, Black-throated Blue, Black-throated Green, and yearling Red-

TABLE 1

ATTENTIVE BEHAVIOR IN EIGHT SPECIES OF WOOD WARBLERS

	Incubation			Brooding			Feeding young					
		Average periods			Average periods*					Times fed		
	Total observation	Attentive	Inattentive	Total observation	On nest	Off nest	Total observation	No. of young	Age of young	♂	♀	Rate per hour
	min.	min.	min.	min.	min.	min.	min.		days			
Black and White Warbler	—	—	—	—	—	—	120	5	4	2	3	2.5
Magnolia Warbler	144	120[a]	20[a]	114	16	6	114	?	0–1	2	3	2.6
Black-throated Blue Warbler	323	28	9	168	19	7	100	4	3–4	6	3	5.4
							105	3	6–7	3	4	4.0
Black-throated Green Warbler	—	—	—	—	—	—	153	?	?	6	7	5.5[b]
Blackburnian Warbler	110	19	11	—	—	—	—	—	—	—	—	—
Chestnut-sided Warbler	266	13	8	170	25	15	84	3	0–1	2	2	2.9
							86	3	3–4	7	4	7.7
	520	21	6	—	—	—	—	—	—	—	—	—
	—	—	—	57	17	6	57	4	1–2	6	6	12.6
Louisiana Water-thrush	—	—	—	—	—	—	53	4	8–9	?	?	7.9
Redstart	119	9	2	—	—	—	—	—	—	—	—	—
	153	18	8	53	15	4	53	4	3–4	12	1	14.7
	—	—	—	—	—	—	94	?	4–8	11	8	12.1

* During the first four days.

[a] Probably not representative for the species.

[b] Includes one additional feeding by an adult whose sex was not determined.

starts) have a wider area—a "home range"—over which they wander, sometimes singing, sometimes not. This wide home range may begin to develop during protracted pre-mating periods but more commonly does so after incubation is begun by the female.

The female takes no part in defense of the male's territory and may disregard its boundaries. However, she vigorously defends a smaller area around the nest, especially during the egg-laying and incubation periods, from both sexes of the same and of other species of wood warblers. This defense is less vigorous after hatching of the eggs. "Injury feigning" behavior may occur in the presence of predators.

The female usually builds the nest alone, although occasionally the male may help. The female is responsible for incubation of the eggs, but the male helps to feed the young. Four days commonly elapse between the start of nest-building and the laying of the first egg. Full incubation behavior is established when the last egg is laid, or occasionally earlier, and the incubation period is normally 12 days long. After hatching, the young remain in the nest 8 to 10 days.

Periods of attentiveness and inattentiveness are well marked, especially during incubation and brooding of the young. In different individuals and species, the average length of the attentive period during incubation varied from 9 to 28 minutes and of the inattentive period from 2 to 11 minutes (Table 1). Brooding and non-brooding intervals vary over approximately the same range. The adult male usually feeds the young at least as frequently as the female and often more frequently, since part of her time is given to brooding. The average rate of feeding varied from 2.5 to 14.7 times per hour.

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NOTES ON THE LIFE HISTORY OF THE MEXICAN VIOLET-EAR

BY HELMUTH O. WAGNER *

THE range of the genus *Colibri* extends from Brazil and Peru to Mexico. In this vast territory there live nine species according to Ridgway (1911:481), six species according to Cory (1918:219–221). The concept of the polytypic species has not yet been applied to the hummingbirds; if it were, several forms of Violet-ear currently called full species would probably be united in one polytypic species, for the differences between the forms are very small. The Mexican Violet-ear (*Colibri thalassinus*) represents the genus in southern Mexico, Guatemala, and El Salvador. Dickey and van Rossem (1938:258) have suggested that it may be conspecific with *Colibri cyanotus*, of Costa Rica, whose range extends south to Venezuela and Peru.[1] Some of the habits of *Colibri thalassinus* seem to indicate that it may have immigrated into Mexico only recently. The following notes on the species were made in the mountains surrounding the Valle de Mexico from 1941 to 1945.

HABITAT

In Mexico the Violet-ear is primarily a bird of the high mountain forest. In the mountains surrounding the Valle de Mexico, the breeding habitat was formerly mixed oak, cypress, and pine woods which extended up the slopes to an altitude of 2,900 meters, but today this habitat is almost completely destroyed. It was replaced by cornfields after the woods had been considerably thinned out by burning for charcoal. The Mexican Violet-ear has adapted itself to the new environment. It is found today not only in what remains of the original habitat but also in the densely overgrown barrancas (gullies) which cut through the cultivated land, as well as in bushes and the occasional high trees at the edges of fields. The males that do not migrate live between breeding seasons in the fir (*Abies religiosa*) forest at 2,900 to 3,500 meters altitude.

In Chiapas I have found the Violet-ear between November and June (that is, between breeding seasons) in open places of the virgin rain forest (2,000 meters), in cypress-pine forest (1,450 to 1,800 meters), and in clearings of the primeval forest at 1,000 meters. The birds visited these different places at different times according to changing weather conditions. The vegetation at these various localities is very different, but the presence of flowers, especially the several kinds of mountain *Salvia*, seems to determine the Violet-ear's occurrence at all of them.

* Translated by Margaret Mayr.

1 In Volume 5 of the "Check-list of Birds of the World," which appeared while this paper was in press, Peters reduces the number of species in the genus *Colibri* to four and lists *cyanotus* as a subspecies of *Colibri thalassinus*.—Ed.

Habits Between Breeding Seasons

In the northern part of its range, north of the Isthmus of Tehuantepec, the Violet-ear is, with some reservations, a migratory bird. The adult females, the young, and some of the adult males migrate after the breeding season. The other males stay as vagrants in the neighborhood of the breeding range. (In a very dry winter, such as 1944–45, they disappear from the area in the second part of February and are not seen again all spring.) Their number varies from year to year. I estimate that from 50 to 90 per cent of the total migrate. In the fall, when the genetically rooted migratory impulse becomes operative, environmental factors determine whether and when migration shall occur; but there is considerable variation in the degree of readiness to migrate, different individuals reacting differently to the same set of external conditions. When in fall, living conditions are relatively favorable, in other words, if the pressure of external factors is not particularly strong, then the percentage of migrating males is smaller than in those years in which the weather at migration time is inclement and the food situation therefore less favorable.

Migration occurs between the beginning of October and early November, always coinciding with a change in the weather for the worse. The migrants return in the second half of July. (In 1942, when in all Mexico the rainy season started four weeks later than usual, their return was delayed two weeks.) It is not known where the migratory Violet-ears are the remaining eight months of the year, but one may assume that they are in Central America. In Chiapas, Guatemala, and El Salvador, more females than males are collected in the months during which the females are absent from their northern breeding range, and this might be explained by the wintering there of the migrating birds from the north.

In the Valle de Mexico proper, I observed Violet-ears only in the months of July and October. They stayed in the oak forests of the Petregals, very near to the Capital, and were probably transients from the northern breeding range. The males made themselves conspicuous with their loud call. I suspect that a bird arrives in one night and departs in the next, since I would observe individual birds only for one day in the immediate vicinity of a given group of trees.

Manuel M. Villado (1873) reported that *Colibri thalassinus* arrived in the Valle de Mexico region in July and left in November. The same was reported by Rafael Montes de Oca (1874). They evidently were not aware that some of the birds did not migrate, and it seems improbable that the Violet-ears could have been overlooked during eight months of the year since they draw attention to themselves even between breeding seasons by their loud voices. Seventy years ago, then, the Violet-ear of the Mexico City region was presumably completely migratory. The reason for the declining intensity of the migrating im-

pulse in at least a part of the population cannot be stated with certainty. The fact that the climate has become warmer and much more arid during this period, probably because of intensive deforestation and the draining of the Texcoco Lake in the Valle de Mexico, may be relevant. Comparison of the data of the above-mentioned ornithologists with my own field observations shows that other species also have changed their migratory habits. With some, we find a considerable prolongation of the time of residence here; others remain throughout the year in varying numbers, as the Violet-ear does.

In winter and spring, the resident male Violet-ear is found where favorable feeding conditions prevail. The effects of the increasing dryness (November to May) are most noticeable at the lower altitudes. Hence we find the Violet-ear during these months above 2,900 meters, especially in the fir forest and in canyons where it is damp even in the rainless season and where the effect of the night frosts is greatly diminished. (In extremely dry winters, as mentioned above, they disappear from the area entirely during the spring months.)

As a rule, several males gather at spots where there are at least a few flowering plants. Such external requirements for life probably bring them together rather than a social impulse. They immediately betray their presence to the observer by their loud voices. During the eight months' absence of the females, the males call loudly and are capable of reproduction, as investigation of the testes proves. They are silent only during the molt in April and on days of inclement weather.

They prefer exposed perches permitting an open view and usually sit high up in a fir tree on a small dry twig while they make their call—the short, continuously repeated, notes are so monotonous that one can hardly call them a song.

The Reproductive Period

Season. As soon as the females arrive in the breeding range at the end of July, they choose a nesting site and begin immediately with the building of the nest. There is only one brood in a season. They attempt to replace lost broods only if the nest is destroyed during the first half of the breeding cycle. Any other course is made impossible by the shortness of their stay (three to four months) and the length of the period between the beginning of nest building and fledging of the young (about two months).

The question remains whether the Violet-ear has a second or even a third breeding season between November and July. Hummingbirds, in contrast with most other birds, are capable of reproduction throughout the year except during the molt. They begin to breed in my observation area as soon as external conditions are favorable. The male Violet-ears that remain in the north during the absence of the females show all the exterior signs of readiness to breed, and the testes produce

spermatozoa. In another species, the White-eared Hummingbird (*Hylocharis leucotis*), which lives in the same region, even some of the females remain through the winter. These reproduce regularly. And young birds have been found in the presumed winter range of the migrants. I collected a bird in that area on April 12 that was still in juvenal plumage. In El Salvador, Dickey and van Rossem (1938:259) collected a young Violet-ear that had just left the nest on February 7, 1925. These young might, of course, belong to indigenous parents, but why should the immigrant birds, which live in the region for eight months of the year, not breed at the same season?

Behavior of the male. The males that spend the winter as vagrants in this neighborhood appear in the breeding range as soon as some of the migrating Violet-ears have come back. They perch by preference in the high cypress trees that rise above the low oak forest and call. I often saw three to five males in a limited area, usually only 8 to 15 meters apart, so that they could hear and see each other. I once observed two calling males perch in the same tree not more than a meter apart for over 10 minutes without paying any attention to each other. Not every bird, then, has his own separate territory. Mutual stimulation among males, that is, an enhancing of sexual excitement, does not seem to occur. The gathering of several males at certain localities is probably due to the especially favorable environmental conditions. Many males stay in the chosen territory during the whole breeding season. Only those that have mated seem to follow their mates into the nesting territory. This attachment to the chosen territory extends apparently not only through one season but also from year to year. One male which could be distinguished from other males by its peculiar call stayed by preference during the breeding seasons of four successive years in the same isolated tree.

As mentioned above, the plant associations of the original breeding habitat have been largely destroyed by the constantly increasing cultivation of the country. The male Violet-ear has adapted himself to the changed conditions in the selection of perching places. Even after cultivation there remain a few high trees, especially where the properties of two owners meet, and such habitats are regularly used by the hummingbirds. Figure 1 shows a typical habitat of this sort in my observation area. In the immediate vicinity of the Capital, adaptation to changed conditions has progressed so far that the males are not only satisfied with isolated trees but even perch occasionally on the tips of corn plants. The density of the male population during the breeding season differs according to local conditions. It was especially dense at the edge of a forest which bordered newly cultivated fields. One morning I saw 27 calling males along a 500- to 530-meter stretch of road, the width of the area where I observed the birds being not more than 100 meters.

The males call continually in the breeding territory to attract the attention of the females. Not only do their calls take three different forms, but the behavior of the bird changes visibly, showing three rising degrees of sexual excitement. This division is, of course, arbitrary, since it is based only on a few conspicuous signs. The three forms of expression may be described as follows:

1. A varied call given while perching on an exposed branch. On different occasions I noted: ***huit ti titatia; huit tita; tetahui tetahui;*** and ***teta tetui tetahui.*** The call is continuous, yet not very intense. A change of perch takes place only when the male visits blossoms in the vicinity to feed. I heard this type of call in the winter, rarely in other seasons except during inclement weather, but always then, when the feeding conditions were not very good.

Figure 1. Type of cultivated area used by the Mexican Violet-ear as breeding habitat since the destruction of the forests.

2. A call with increased intensity and strength of tone as compared with the preceding: ***ahuit ahuit ta ta; huita huita; huit ti ta huit ti ta.*** The male turns his head slowly from one side to the other while calling. He changes his perch frequently from one tree to another, on the average, every two minutes, forty seconds (between 1 minute 35 seconds and 4 minutes 10 seconds). During the flight, which is slightly undulating (Figure 2), he is silent, but otherwise he rests from calling only to satisfy briefly his need for food. One hears this type of call when living conditions are favorable, especially during the first week after the females have arrived.

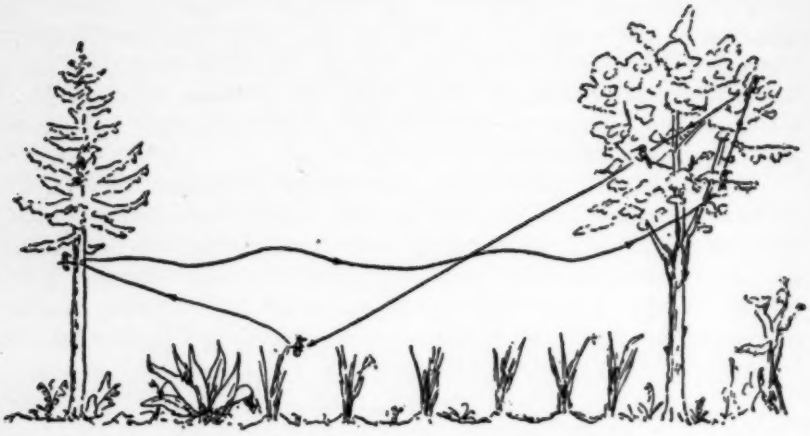

Figure 2. Perches used by a male Violet-ear while giving his call. Change of perch between calls regularly followed the sequence shown.

3. A continually repeated *huitta huitta,* expressing the peak of sexual excitement, and audible at distances of 80 to 100 meters. While perching, the bird turns his head continually from one side to the other as he sings. At the same time the head feathers—and in the highest ecstacy, the feathers of the back—are raised. The tail seesaws up and down restlessly. He changes his place continuously from one twig to another in the crown of a tree or from one tree to another. On stretches of more than 20 meters, the flight is undulating in both the vertical and horizontal planes. During the flight, he utters a call: *itta itta* or (more rarely) *huita huita.* This call is strong, though less loud than the call from a perch. When the male alights on a twig he keeps his wings spread and quivering for several seconds. Very rarely one sees the same quivering and spreading of the wings in a bird that has been sitting with folded wings for a few minutes.

On August 27, I recorded the alternating singing and feeding periods for the space of over an hour as shown in the accompanying table.

Singing period		Feeding period	
		1 min.	55 sec.
10 min.	40 sec.	1	55
5	15	3	10
18	50	2	05
3	00	1	05
6	45	1	10
8	10	1	55
52 min.	40 sec.	13 min.	15 sec.
Av. 8 min.	46 sec.	Av. 1 min.	53 sec.

I found the third and highest degree of excitement only in the breeding territory and after the females had finished nest building and were looking for mates. It seems to occur only under the influence of the female. As sexual excitement increases, the males become more wary. If one approaches within 40 or 50 meters of them they leave their perch.

The males call during the whole day but become quieter in the afternoon, especially in the winter months. If the weather is cold and rainy, or even cloudy, the intensity and duration of the calling are considerably diminished.

In some places the breeding territories of the Violet-ear and the White-ear overlap. One then often sees males of the two species only 10 to 15 meters apart in cypress trees, calling loudly and paying no attention whatever to each other. There is, however, a change in this behavior when two birds come to the same flower to feed during an intermission of their calling. Then the smaller White-ear is immediately driven away.

Relations between the sexes. The Mexican Violet-ear belongs to the group of hummingbirds in which the mature females, after building the nest, search for the males. The males advertise their presence and gain the attention of the female by their loud voices and by display flights. (Most of the other hummingbirds in Mexico use only one of these two methods.) In the Violet-ear, it is primarily the far-reaching call that draws the attention of the females, but I am sure that the undulating flight during the change of perch has also a certain importance.

My knowledge of the courtship flight that precedes copulation is incomplete. It is based on a series of separate observations made over a period of years. I have combined these to make up what I suppose to be the sequence of the courtship ceremony. It would probably be impossible to observe the sequence as a unit since the various steps or phases take place at different localities. Since the sexes in the Violet-ear look alike, the identification of male and female in the following description of the courtship ceremony are based on my own assumptions.

1. When the nest is nearly completed, the female, now ready for fertilization, looks for places where males are calling. As soon as she comes in view she is followed by one or more males. When two or more males follow a female they begin a wild race, but as soon as one male reaches the side of the female, the other males drop out and return to their territory. Single males meeting a pair flying side by side pay no attention to them.

2. The pair fly side by side not more than 50 centimeters apart. In a fluctuating wavy flight they pass and repass a certain stretch (300-500 meters ?) which seems to be the nesting territory of the female. During the flight a soft *zesesoorr* is audible. Apparently in the later flights

they sometimes clap their wings, since they make a sound like that made by pigeons. At one of the two end points of the stretch, the flight is interrupted for two or three minutes, while the female goes down in the same tree crown and flutters around with a low *tick tick tick*. The two mates are not together during this time, and I do not know what the male does. Suddenly he appears again flying directly past the female, who follows immediately. The stretch is flown in each direction at least five times.

3. The sexual excitement of the female has increased with each trip. Finally, at one of the end-points of the stretch, it reaches its climax. She descends from the top of the tree in a fluctuating, wavering flight, with loud wing-clapping; on nearing the ground she flies upward again and perches for a short time on a twig. She repeats this until the male again appears and leads the female in a final wild flight.

4. I did not observe copulation, which presumably follows this display. It does not seem to take place in the vicinity of the nest. I once had occasion to observe the second phase near a nest which presumably belonged to the participating female. About 20 minutes after I last saw the birds, the female returned to the nest. Two days later the nest contained its first egg.

As a rule in hummingbirds, the male pays no attention to the female after mating. Incubation and care of the young are solely the concern of the female. In the Mexican Violet-ear, although I commonly observed a single calling male in the vicinity of a nest, there was no evidence of his relationship to the owner of the nest. Robert T. Moore (1939:315—also Bent, 1940:471) reports, however: "In Ecuador I have observed the male and female [Lesser Violet-ear, *Colibri cyanotus*] take turns incubating at the same nest and collected both sexes to substantiate this observation."

Nesting territory. In the selection of nest sites, the females have adapted themselves to the changed conditions of their habitat as the males have in selecting singing perches. Only two of the eight nests I found from 1941 to 1943 were situated in the oak-cypress forest; the others were in densely overgrown barrancas, 20 to 30 meters wide, surrounded by cornfields. In the barrancas, whose slopes are too steep for cultivation, one often finds small oak shrubs among the dense bushes. The site originally preferred seems to have been a free oak branch (*Quercus crassipes* or *Q. nitens*) about 40 to 180 centimeters above the ground. I found five nests in such situations (Figure 3). Another nest was in the dense branches of a small oak (2½ to 3 meters high) which had grown up from an old root (the site shown in Figure 7). With the other two nests, however, the plant associations of the habitat, as well as the "nest tree," were entirely different. Each of these nests was built in the vertical fork of a stem of *Salvia polystachya* among the bushes of a barranca (Figure 4). The plants could barely support the nests and were saved from breaking only by the dense plant growth around them.

Figure 3. Nest of a Violet-eared Hummingbird on the twig of an oak (*Quercus nitens*).

Figure 4. Nest of a Violet-eared Hummingbird on a stalk of sage (*Salvia polystachya*).

Every female has a strictly defined territory in which no other female of the same species is tolerated. Surrounding the territory is a "neutral zone" in which neighboring females do not fight when they meet. Apparently the male stays in this zone also, and avoids if possible the nest territories, even the one belonging to his own mate. I was able in 1942 to determine quite accurately the size and boundaries of the nesting territories. In that year I found four nests of the Violet-ear that were occupied at the same time. They were nearly in a

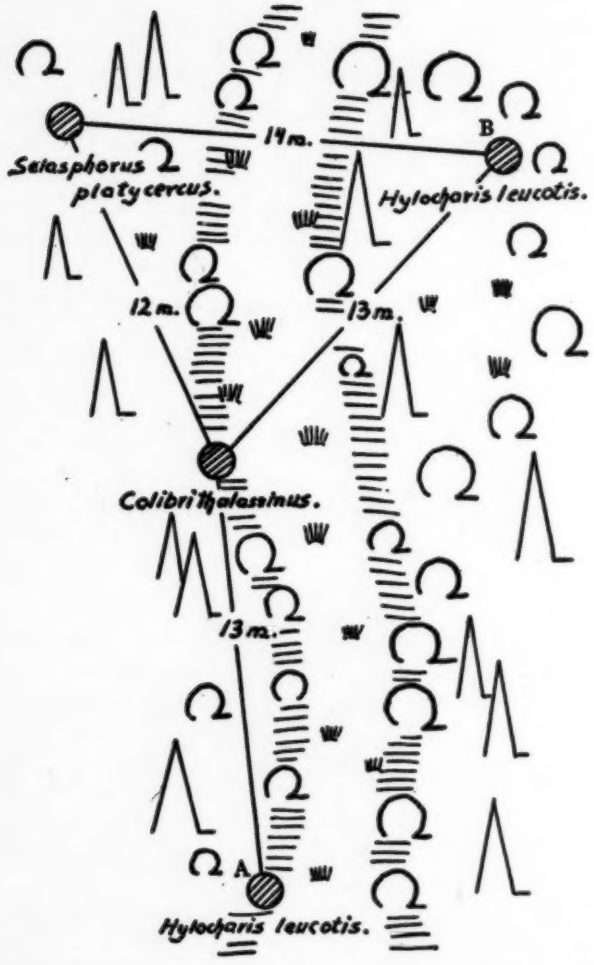

Figure 5. Location of nests concurrently occupied by three species of hummingbird (*Selasphorus platycercus, Hylocharis leucotis, Colibri thalassinus*). Distribution of vegetation shown schematically. Distances in meters. Nest B of *Hylocharis leucotis* was probably a substitute for Nest A, which had been destroyed.

straight line, three in an overgrown barranca, the fourth higher up, at the edge of a thin oak-cypress forest. The nests were 52, 60, and 95 meters apart. There were natural boundaries between the nesting territories since the dense flowering growth of *Salvia mexicana* was pushed back by higher bushes and trees even at the foot of the barrancas. Each of the nesting territories comprised an area of 600 to 1,000 square meters. The "neutral zones" around them were mostly border-strips where the vegetation of the barranca bordered on the cornfields. There are no flowering, food-bearing plants whatever in the cornfields, and they are therefore not visited by the Violet-ears. Birds that nest in the forest, where the flower growth is more sparse, apparently have much larger territories. Except for some *Salvia cardinalis* growing in the shady, damp places, *Pentstemon campanulatus* is the only one of the flowering plants in the forest that is visited by the hummingbirds.

The Violet-ears pay no attention to other species of hummingbirds that breed in the vicinity of the nest. In August, 1941, I found in a very restricted area a nest of *Colibri thalassinus*, one of the White-ear (*Hylocharis leucotis*), and one of the Broad-tailed Hummingbird (*Selasphorus platycercus*). All three nests were occupied at the same time, although the different species were at different stages of the reproductive cycle. The young of the Violet-ear hatched August 18; the young of the Broad-tailed Hummingbird left the nest about four days later, while the White-ear was still incubating the eggs. Figure 5 shows the locations of the nests and the distances between them. I never observed that the three female hummingbirds, whose territories partially overlapped, bothered each other. A nest of the White-ear was destroyed by the Violet-ear, but apparently not because it was the nest of another species, but merely to obtain material for her own nest.

The construction of the nest. The nest of *Colibri thalassinus* can be distinguished from all other Mexican hummingbird nests by the long grass hanging down from it (Figures 3 and 4). It is always built at the base of a fork on a slender twig. The structure of the nest is shown in the schematic vertical section, Figure 6. It is built mainly of moss, which the bird picks from the bark while hovering before the branches. Only after the main body of the nest is completed does the bird add the dried grass. The amount of grass used varies. Some nests are densely covered with grass; others show moss in places. The wide grass blades hang down freely to a length of 20 centimeters. The inner lining is usually of moss; sometimes a few feathers are also used but too few to be of importance. Great quantities of spider-web give the structure the necessary coherence. When the nest is finished it is connected with the neighboring twigs and leaves by a great many threads, but it is probable that these are blown there by the wind and not purposely arranged by the builder. By the time the young are hatched, almost all the threads are torn and hardly recognizable.

Once in a while plant down is used for the inner lining instead of moss. This down is the fine "hair" that covers the gall of the oak-gall wasp. It is surprising that the Violet-ear does not itself pick this material from the galls but steals it from neighboring nests of the White-ear. I observed the robbery and the destruction connected with it in three nests. Two of the Violet-ear nests that I found were lined with plant down obtained this way. Figure 6 shows the structure of such nests. The robbing of a nest of the White-ear usually takes place when it is least guarded—in the last days of the construction period or after the young are two weeks old. As soon as the owner of the nest appears, the Violet-ear departs without the least attempt to fight.

If the nest of the White-ear is not finished, she continues to build on it for two or three days until it collapses. She does not mend the damage. If young are in the nest, they stay there until the last pieces are picked away from under their bodies and they fall to the ground. For five days I observed very closely the destruction of a nest with young. One young, 18 days old, fell on the fourth day; the other, a stronger bird, fell one day later. Both died. To get to the dense inner lining of plant down the Violet-ear picks a hole about eight or nine millimeters in

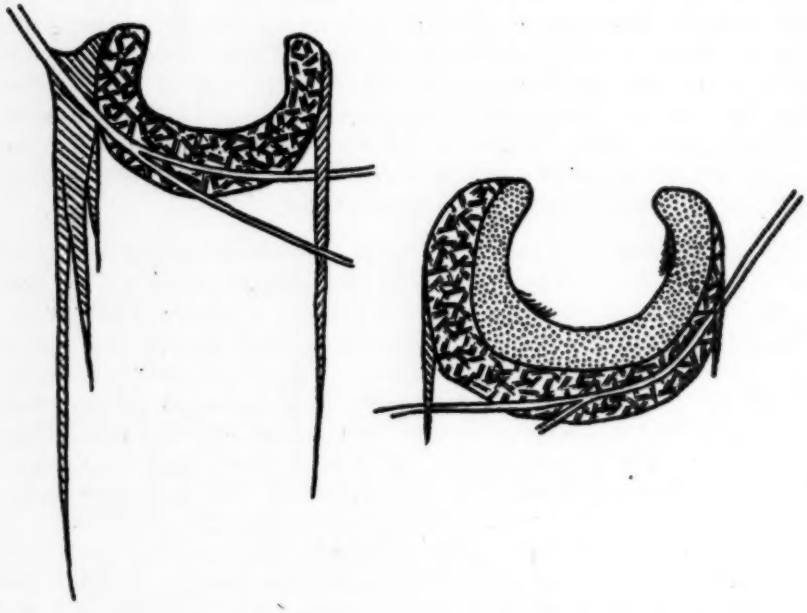

Figure 6. Cross sections of Violet-eared Hummingbirds' nests and supporting twigs, showing the basic structure of moss and hanging grass. Nest on left is lined with moss, nest on right with plant down stolen from a White-eared Hummingbird's nest. Spider web is used as a binder.

diameter in the side of the moss wall. In a short time the nest collapses. Later, the Violet-ear steals the moss also, until only a few remnants remain. While picking the material, the Violet-ear usually hovers before the nest. But if there is an opportunity to perch on a twig, she does so.

The nest of the Violet-ear is by far the most compact of all the hummingbird nests that I have had the opportunity to examine closely. Even by the time the young leave the nest, it has merely been stretched larger; the walls are not deformed or torn as is the case with many other species of hummingbird whose young in the last days rest on the platform-like ruins of a nest.

Incubation. I only once found a nest of the Violet-ear early enough to determine the exact period of incubation. The young hatched between the sixteenth and the seventeenth day. After laying the first egg, the bird sat on it for several short periods during the forenoon. This beginning of incubation before the clutch is complete seems to be the reason that the eggs hatch at different times.

After the clutch is complete, the bird leaves the nest only for short intervals to look for food. On the third day of incubation, she left every 24 to 30 minutes for periods of 9½ to 14½ minutes. As the day of hatching approached, her feeding time became shorter. On the twelfth day, that is, four days before hatching, the bird left the nest every 18 to 25 minutes for periods of only 3 to 4 minutes. On the last day she stayed away for scarcely 2 minutes at a time.

During the breeding season, the Violet-ear is, as a rule, extremely wary around the nest, but there are great differences among individuals. Usually the bird flew off when I had approached carefully to within 8 to 15 meters. She left stealthily and without a sound. When about 20 meters away she would start calling anxiously. The female always takes the same route to and from the nest, whenever possible one concealed by vegetation. One bird that regularly visited flowers within a meter's distance in full view of her nest, did not take the direct route in returning to the nest but went a round-about way, circling a bush to reach the point from which she regularly made her approach to the nest. Before going to the nest, a female usually perches on a certain twig and reconnoitres. Figure 7 shows the regular route of one female. She always approached through the dense vegetation at the base of the small oak in which the nest was situated, moving upward by several stages to the nest.

While there are eggs in the nest, the bird descends on them without first perching on the edge of the nest or on a neighboring branch. She hovers for several seconds about 10 to 15 centimeters (4 to 6 inches) above the nest, then descends by degrees and suddenly sits on the nest. This happens so fast that one cannot see all the movements in detail. She always sits on the nest facing in the same direction and this determines the direction of approach. After settling on the nest she moves

about a little and then remains almost motionless. When something disturbs her, she moves her head restlessly from side to side, then usually flies off suddenly. The departure is in the opposite direction from the arrival. The bird rises from 4 to 6 inches in the air, hovers over the nest for a moment, and then darts forward.

An incubating bird closely watches birds of other species that come into the neighborhood of the nest but does not chase them away. A female flew off immediately, however, upon seeing a weasel pass underneath the nest site.

Rearing the young. The interval between the hatching of the two young may be as much as 24 hours. The first young to hatch is fed before the second has left the egg. The parent bird does not remove the pieces of eggshell; one can still see them at the bottom of the nest several days later.

Figure 7. Regular flight routes used by a female Violet-ear when approaching and leaving her nest in a small oak 2½ to 3 meters high. Below, route of approach; above route of departure.

The feeding and brooding of the young follow a certain rhythm that changes with the age of the young. As the young develop, the time spent brooding becomes shorter and shorter (usually ceasing after the tenth day regardless of weather conditions), while the time spent looking for food becomes longer. This changing rhythm is illustrated in Table 1. The observations were made at the same nest in the early morning hours. When I arrived at the nest the temperature was between 8° and 10° C. and rose by noon to 12° or 14°. With the exception of a few afternoon showers, the weather during the period was very favorable for the development of the young.

TABLE 1

CARE OF YOUNG

Periods of Absence, Feeding, and Brooding in Minutes and Seconds

Second day			Fifth day			Eighth day			Eleventh day		
Absent	Feeding	Brooding	Absent	Feeding	Brooding	Absent	Feeding	Brooding	Absent	Feeding	Brooding
——	——	14′ 55″	2′ 30″	——	6′ 30″	18′ 37″	0′ 48″	9′ 14″	20′ 55″	0′ 57″	——
8′ 50″	0′ 27″	9′ 03″	7′ 41″	0′ 35″	5′ 25″	16′ 20″	0′ 41″	0′ 07″	22′ 08″	1′ 63″	0′ 35″
7′ 10″	——	11′ 30″	11′ 13″	0′ 50″	5′ 45″	21′ 12″	1′ 00″	0′ 18″	29′ 23″	0′ 45″	——
9′ 40″	0′ 35″	8′ 05″	12′ 18″	0′ 48″	7′ 24″	30′ 54″	0′ 56″	10′ 19″	25′ 06″	0′ 49″	——
5′ 15″	0′ 30″	7′ 12″	7′ 21″	——	9′ 17″	——	——	——	——	——	——
11′16″	0′ 29″	7′ 29″	13′ 18″	0′ 47″	——	——	——	——	——	——	——
Av.: 8′24″	Av.: 0′ 30″	Av.: 9′ 42″	Av.: 9′ 03″	Av.: 0′ 45″	Av.: 6′ 52″	Av.: 21′ 43″	Av.: 0′ 51″	Av.: 4′ 59″	Av.: 24′ 33″	Av.: 0′ 53″	

Fifteenth day			Eighteenth day			Twenty-second day		
Absent	Feeding	Brooding	Absent	Feeding	Brooding	Absent	Feeding	Brooding
39′28″	0′ 54″	——	——	0′ 54″	——	——	0′ 22″	——
29′11″	0′ 47″	——	40′ 28″	0′ 51″	——	6′ 30″	0′ 27″	——
33′47″	0′ 42″	——	36′ 51″	0′ 33″	——	6′ 25″	0′ 19″	——
32′10″	0′ 57″	——	41′ 17″	0′ 55″	——	6′ 06″	0′ 21″	——
——	——	——	——	——	——	6′ 09″	——	——
Av.: 33′39″	Av.: 0′ 50″		Av.: 39′ 32″	Av.: 0′ 48″		one young leaves the nest		
						——	0′ 19″	——
						17′ 51″	0′ 21″	——
						12′ 58″	0′ 24″	——

During the first days after the young hatch, the female does not always feed the young on her return to the nest. Then she has presumably looked for food just for herself. In such cases, the time of her absence is considerably shorter. Other species of hummingbird in the high mountains regularly show this behavior. The White-ear, for instance, during the first week after the young hatch always collects the food for herself and for the young at separate times. This may be connected with a difference in nutrition needs, but I think it more prob-

able that it is an adaptation to the cold weather. The periods of absence are shortened by the separate feeding, and thus the young do not get so cold. In *Colibri thalassinus,* the development in this direction is only beginning. Its habits and degree of adaptation to local conditions indicate over and over again that the species has spread into the north only in recent times.

The day that the first young flew from the nest, the mother bird returned to the nest on the average every 6 minutes, 17 seconds. She would be able to find little food in this short time, and the feeding was accordingly very brief. It is possible that this habit is based on an inner restlessness which is transmitted from the young to the mother. After one of the young has left the nest the two birds are fed alternately, and the female visits the nest only half as often as before.

The table shows that on the eighth day, the female brooded twice for an unusually long period. On this morning the temperature was exceptionally low (8° C. at 9 o'clock, 11° at 11:00). Since at this stage of the young's development, the female stays away for a relatively long time searching for food, the young become rigid with cold when the temperature is unusually low, and they do not take the offered food. In such cases they are brooded longer. This was observed also with other species of hummingbird. The time the female broods is probably regulated by her hunger. When she eats the food intended for the young, the releasing factor that causes her to leave the nest is delayed. Thus is brought about a simple but very important regulation of brooding time according to increased need. The time spent in the actual feeding shows very little variation at different ages of the young. The amount of food given increases steadily, but in the beginning, the young take it in smaller portions, thus effecting a balance.

The Violet-ear feeds her young with the same food that she eats herself. During the first few days, small pieces of animal matter are usually fed, but it is amazing what large pieces can be taken even at that early stage. I did not find honey in crops of the young, but it may be assumed that they are fed it in small quantities to satisfy the need for liquids. The brood is fed regularly throughout the day until it is nearly dark. Feeding takes place from the edge of the nest, always from the same place. Once, however, when the young were rigid with cold and not eating well, I observed the female try to feed them after she sat on the nest. At each visit the female feeds the two young alternately three or four times. The food is collected in the crop and regurgitated in small portions. The touch of the adult's bill to the corner of the young's bill is enough to make the still blind young open its mouth. One gets the same reaction with the tip of a pencil. Touching any other part of the body does not cause them to open the bill. After the young can see, they open the bill as soon as the mother appears at the edge of the nest. The female puts her bill deep into the crop of the young to feed them, remaining in that position from two to four seconds. At

first the feeding is done from above the head of the young. Later, when its bill grows larger, the young bird turns its head and is fed from the side. After nest leaving, the young are fed by their mother while sitting beside her on a branch. She still feeds from the side, so that her head lies between the mandibles of the young as she inserts her bill deep into its crop and regurgitates the food in several portions.

On the second, or at latest, on the third, day after leaving the nest, the young begin to hunt their own food, but they are still fed by the mother as well. It is very surprising to see a hummingbird that is hovering expertly in front of a flower, suddenly interrupt this activity to be fed by another bird. After five to seven days, the young are completely independent.

I have never heard any sounds from the young during the first week after hatching. Later, they peep occasionally. They invariably peeped when I took them from the nest to measure them, but I observed no connection between the sounds and the appearance of the adult at the nest.

The young are very sensitive to heat from the sun. At the time the nest site is chosen, it is in shade all day. But since the birds cannot take into consideration the continuous change in the sun's position, it sometimes happens that later in the season the nest is exposed to the sun. As soon as the sun rays reach the nest, the young begin to pant, even if the temperature is below 10° C. in the shade. With wide open bill, they stretch the head upward and swing it from side to side. If the female returns, she stays at the edge of the nest after feeding the young, restlessly moving back and forth so that the young are in the shade. Very rarely she sits over them, forming a roof against the sun. On such occasions I could see the heads of the young protruding on the shady side. So long as the brood pants, the mother does not fly away whatever their stage of development, but protects them from the sun. Their sensitivity to the sun decreases as they grow older. Even the adult Violet-ear can stand the bright sun only for a short time. The female pants occasionally while protecting the young from the sun. She opens the bill, dropping the lower mandible at an angle of 10 to 15 degrees, and becomes extremely restless.

When it rains, the female goes to the nest and protects the young. In the high mountains of Mexico, during the breeding season, it rains almost every afternoon. By that time the young have received plenty of food. The crop contains four to six times as much as the stomach can hold; hence they can live several hours without being fed and suffer no ill effects. However, if it rains continuously for several days as it did, for example, in 1941, most of the broods perish. The impulse to protect the young against the rain—a very good adaptation to the usual short heavy showers of the tropics—apparently prevented the parent birds from giving the young sufficient food under those unusual conditions.

From at least the fourth day, the young void over the edge of the nest, pushing the body upwards against the side of the nest to eject the feces. I did not observe any correlation between the times of feeding and voiding.

Development of the young. The length of time required for the young to develop sufficiently to leave the nest varies considerably—between 19 and 28 days. Environmental factors greatly influence growth; the most important is the quantity of food that the female procures for the young, and this depends on weather conditions. The various stages of development are apparently reached after given amounts of food are consumed. Differences in rapidity of growth are less pronounced between the broods of one breeding season than between broods of different years with widely differing weather conditions.

In general, the organs develop at a uniform rate. Only under extremely unfavorable conditions are some backward in development; and then the head seems to be less affected than the extremities or feathers. Figure 8 illustrates the difference in rate of growth under

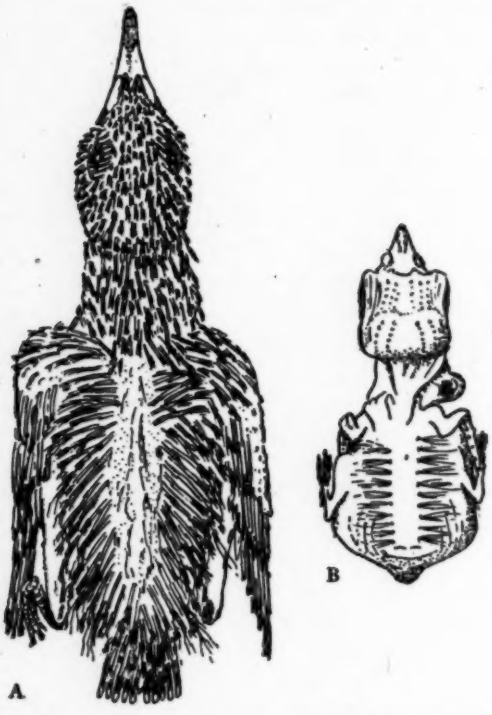

Figure 8. Two nestlings of about the same age (13 to 14 days). Young A (5.85 grams) was sole occupant of nest and developed under optimal weather and feeding conditions (season of 1943). Young B (1.10 grams) shows stunted condition at death after two weeks of malnourishment due to extremely severe weather (season of 1941).

different environmental conditions. Nestlings A and B are about the same age—if anything, the less-developed one is a little older than the other. I am comparing here the greatest extremes that I could find. The two birds were collected in the same area but in different years.

Nestling B had lived under the worst conditions imaginable. For two weeks after hatching it did not grow at all but merely subsisted. These two weeks were unusually rainy, and thus the mother was prevented from looking for food for long periods, and when she went for food she needed much more time than normally because of the unusually cold weather. The young bird shown here, as well as the other member of the brood, died after these two weeks of malnutrition. When I found them, they had just died, and the mother was still coming to the nest, trying to feed them. There were a few insects in the stomachs and crops. The nestlings weighed 1.10 and 1.05 grams. Their eyes were still closed.

Nestling A was the only occupant of its nest. I collected it when it was 13 to 14 days old. Every part of the body was much more highly developed than in Young B. It was covered with sheathed feathers in contrast with the other, which showed scarcely more than an indication of the feather tracts. The eyes had been open for 6 days. The weight was 5.85 grams, five times that of Young B.

Under normal conditions, if the brood consists of two young they leave the nest between the twenty-third and twenty-fifth day. A single nestling receives a double portion of food and grows considerably faster. Twice I watched the growth of neighboring broods, one with one young, the other with two. In one case, the single young left the nest four days earlier than the other two young, at 19 to 20 days. (The young left the nest on my approach. I had not handled it.) The longest time in the nest I have recorded was 27 to 28 days. In that case, a few rainy, cold days had inhibited the growth. Possibly under worse conditions, the time required for development might be even longer.

These facts help to explain the variation in the figures given in the literature for the nestling period of hummingbirds of a given species. One must assume that this period is also dependent on the length of day, varying with the time of year and the latitude.

The following notes, made on a brood of two at 3-day intervals, illustrate the normal progress of the young Violet-ear's development.

2nd day: 12 and 36 hours old. Upper parts, graphite black; lower parts, flesh color; at sides, gradual transition from one color to the other. Eyes closed. On the back, two rows of 10 to 12 down feathers (Figure 9), each 4 to 5 mm. long. (The number of down feathers is often not the same at the two sides.) Bill, light yellow; 3.5 mm. wide, 3.3 mm. long.

5th day: Color unchanged. The first signs of the contour feathers showing on the head as small papillae. Bill and body considerably larger, but unchanged in proportions.

8th day: Both young had grown so much that they filled the nest completely to the brim. Some sheaths were beginning to open on the head, showing the tips of brown feathers. Back covered with sheathed feathers, the primaries 2 to 3 mm., the secondaries just visible. No tail feathers visible. Bill longer, its tip darkening to black. One bird opened one of his eyes in a narrow slit when I pulled out a sheath.

11th day: The eyes had opened though they were kept closed most of the time. The whole upper parts were covered with sheathed feathers, those on the back beginning to open. At the sides of the body, a slight trace of feathers. Very short sheathed feathers on the tail. (The down feathers remain for several days at the tips of the opening sheaths.) The young no longer opened their bills when touched. The lining of the throat and mouth was orange-red with yellow border.

15th day: The growth of the body (except the chest) now almost complete. The sheaths were open over the whole of the upper parts. The feathers at the sides of the chest were beginning to appear. The primaries were 14–15 mm. long, the distal 4 mm. unsheathed. The sheathed tail feathers (5.2 mm. long) were just about to open. The feathers on the head had grown very little since the seventh day. The feathers of the back still had down at their tips. Bill, 6.7 mm. long. From the tip of the bill along the culmen, the color was progressively darkening to black. The tip was now completely black, the edges of the mandibles still yellow.

18th day: The young were completely feathered. Primaries, 22–25 mm., of which 12–15 mm. were unsheathed. Tail feathers, 10 mm., of which 3–4 mm. were unsheathed. The tips of the wings were even with the tip of the tail.

22nd day: All the feathers were entirely unsheathed. The brown edges of the contour feathers were already wearing off. The blue ear patches had begun to show. Length of culmen, 10.4 mm. (The bill of a full-grown Violet-ear in this area has an average length of 18.4 to 18.8 mm.) The bill was all black, only the corners showing a little yellow. While I was watching, one bird left the nest; the second one stayed for another day.

Figure 9. Down feather of nestling Violet-ear. 20 times natural size.

The period of development is, in general, divided into two phases. In the first phase—up to the fifteenth day—the body increases continuously in weight, but the growth of the feathers is very slow. In the second phase, hardly any gain in weight takes place, but the feathers and bill develop.

Unfortunately I was not able to record the gain in weight of the same individual. The following weights are from different birds:

Nest 2, 1941	(Nestling B, Figure 8)	14 days	1.10 grams
	(nest-mate of above)	14 days	1.05 grams
Nest 1, 1943	(Nestling A, Figure 8)	14 days	5.85 grams
Nest 2, 1943	(♂)	17 days	5.85 grams
Nest 2, 1943	(♀)	17 days	5.45 grams

For comparison, a few weights of full-grown birds:

♂ juv. November 2	5.30 grams
♂ ad. December 29	5.65 grams
♂ ad. January 8	5.65 grams
♂ ad. January 9	5.15 grams

The greatest weight I recorded was for two nestlings of 5.85 grams each, one 14, the other 17 days old. They were equally well developed externally. The greatest weight I recorded for adults was 5.65 grams (two males). A female of a brood is usually a little lighter in weight than a male of the same brood. Thus under normal conditions the nestlings reach the weight of the adults, or even go beyond it, after two-thirds of their nestling period. Their form, however, is very different from that of an adult, as shown in Figure 10.

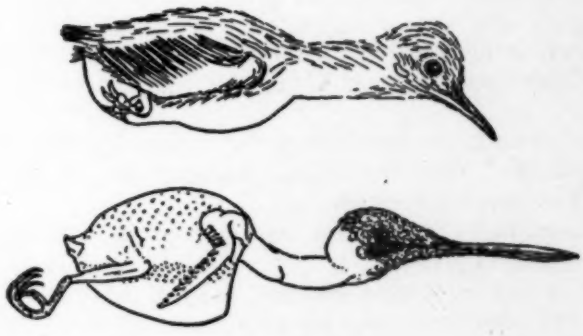

Figure 10. Nestling and adult Violet-ear. Nestling (age 17 days): 5.85 grams. Adult (collected January 9): 5:10 grams. The adult was plucked to show the body form.

Speed of Flight

The speed of the hummingbird's flight varies with circumstances. It was possible with a stopwatch to make numerous measurements of the male Violet-ear's speed as he made his regular flights from one isolated tree to another while calling to attract the female. He attained an average speed of more than 90 km. per hour. This speed, however, is considerably lower than his maximum, which I estimate may be twice as high. On the occasion of one Violet-ear chasing another, I noted a velocity of more than 150 km. per hour. Since this is only a single observation, the record is not absolutely dependable. When the bird passes close by at high speed, one hears a noise like the snap of a whip. The speed of its reactions and its versatility in flight are astonishing.

Summary

The Mexican Violet-ear (*Colibri thalassinus*) is primarily a bird of the mountain forest. Its breeding habitat in the mountains surrounding the Valle de Mexico is the oak-pine-cypress forest. Since the destruction of the forest and the cultivation of the land, the Violet-ear has adapted itself in some degree to the new environment.

In its northern range the Mexican Violet-ear is in part a migratory bird. The females, the young, and a varying percentage of the adult males go south in October and early November and return to their breeding range in July. The presumed winter range is in the mountains of Chiapas, Guatemala, and farther south. Environmental conditions greatly influence the percentage of males that migrate, as well as the time that migration takes place. According to reports from 1873 and 1874, all Violet-ears then migrated in winter. The non-migratory males usually stay as vagrants in the fir forest (2,900 to 3,500 meters) at places where there are flowering plants even in winter. In dry winters, however, all the males leave the area by the second half of February.

Immediately after their return in July, the females begin building the nest. There is but one brood. Substitute broods are attempted only if the eggs have been destroyed during the first half of the breeding cycle.

The males attract the attention of the females by their loud calls and display flights. There are several phases of song, expressing different stages of sexual excitement.

After completing the nest, the females look for the males, and courtship flight takes place.

The nest is usually situated low down in small oaks. As an adaptation to the new conditions, other low plants are also used. The nest is easily identified by the long grass hanging down from its sides. The most important building material is moss. Occasionally the Violet-ear steals nesting material from the nest of the White-eared Hummingbird.

The young hatch after an incubation period of 16 to 17 days (determined at only one nest). They leave the nest after 19 to 28 days (sometimes possibly more—under normal conditions they leave after 23 to 25 days). They are fed for 5 to 7 days after leaving the nest. In general, a period of 55 to 65 days is required for the nesting cycle—from the beginning of nest construction to the complete independence of the young.

The rate of growth of the young is largely dependent on the weather. Therefore the degree of development at any given age shows a marked variation.

The speed of flight is, under normal conditions, more than 90 kilometers per hour. This can be accelerated to more than 150 kilometers per hour (recorded in one instance).

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THE OCCURRENCE OF THE INCUBATION-PATCH IN SOME BRAZILIAN BIRDS *

BY DAVID E. DAVIS

FROM September 1942 to January 1943, a series of more than a thousand birds was collected at Teresopolis, State of Rio de Janeiro, Brazil, for the purpose of determining the breeding season. In addition to the usual data (date of collection, locality, etc.), the presence or absence of an incubation-patch and the age (as determined by the ossification of the skull and the size of the bursa of Fabricius) were noted. The sacrum of each individual was cut out and preserved in Bouin's fluid. The gonads were removed under a dissecting-scope and sectioned for an accurate determination of the breeding condition. The patch was considered present in the species if present in one or more individuals of either sex in active breeding condition; absent in the species if absent in two or more individuals in active breeding condition.

Brood- or incubation-patches are "specially modified areas of bare skin" which are "adaptations providing for the closest possible application of the eggs to the warm surface of the body, and, what is more, to an area rendered particularly suitable for the purpose by a heightened blood supply and other changes. . . ." (Tucker, 1943:22). Although not all species of birds have the patch, the majority do, and the patch is obviously an important factor in incubation (Ryves, 1943:10); in some species only one sex has the patch, and its presence (or absence) may be used in the determination of sex (Nice, 1937:4; Kendeigh, 1941:11).

The patch occurs only in the breeding season: species and sexes that showed patches in the breeding season showed none in the non-breeding season; and no individual with inactive or progressing gonads showed the patch. The occurrence of the patch in the series studied is shown by sex and species in Table 1. The patch was found in one or both sexes of 43 species (representing 16 families). In no species investigated was the patch absent in both male and female, but both sexes were not collected for all species.

The occurrence of the patch invariably agreed with the incubation habits when these were known. Ticehurst (1931:582–583) determined the occurrence of the patch in 35 species of shore birds and found almost perfect correlation with what was known of the incubating habits. So very few Brazilian birds have been intensively studied that it is not yet possible to completely correlate the occurrence of the patch with in-

* The work on which these observations are based was done under the auspices of the Serviço de Estudos e Pesquisas sôbre a Febre Amarela (Yellow Fever Research Service), which is maintained jointly by the Ministry of Education and Health, of Brazil, and the International Health Division of The Rockefeller Foundation. The collection of the birds here reported upon was part of an investigation of the ecology of the forests in relation to jungle yellow fever (Davis, 1945). The skins have been presented to the Museu National, Rio de Janeiro.

TABLE 1

THE OCCURRENCE OF THE INCUBATION PATCH IN MATURE BREEDING SPECIMENS OF SOME BRAZILIAN BIRDS

		Present		Absent	
		♂	♀	♂	♀
Tinamous (Tinamidae)	*Crypturellus obsoletus*				2
Parrots (Psittacidae)	*Pyrrhura frontalis*			2	
Cuckoos (Cuculidae)	*Piaya cayana*	1			
	Guira guira	2	1		
Hummingbirds (Trochilidae)	*Eupetomena macroura*	1			
Trogons (Trogonidae)	*Trogonurus rufus*	1	1		
Woodhewers (Dendrocolaptidae)	*Xiphocolaptes albicollis*	2	2		
	Lepidocolaptes fuscus			5	
Ovenbirds (Furnariidae)	*Certhiaxis cinnamomea*		1		
	Syndactyla rufosuperciliata	2	2		
	Automolus leucophthalmus			3	
	Cichlocolaptes leucophrys	1			
	Heliobletus contaminatus		1		
	Sclerurus scansor	2	1		
Antbirds (Formicariidae)	*Batara cinerea*		2		
	Drymophila ferruginea	1			
	Drymophila milura	1			
	Pyriglena leucoptera	1			
	Myrmeciza loricata	1			
Cotingas (Cotingidae)	*Attila rufus*		2		
	Pachyramphus polychopterus			2	
	Tityra cayana	1	1		
	Procnias nudicollis			2	
Flycatchers (Tyrannidae)	*Myiodynastes solitarius*	1	1		
	Myiozeteles similis		1		
	Empidonax euleri	1	1		
	Myiobius atricaudus		1		
	Onychorhynchus swainsoni		1		
	Hemitriccus diops			4	
	Elaenia mesoleuca		1		
	Phyllomyias griseocapilla	1			
Wrens (Troglodytidae)	*Troglodytes musculus*		1		
Mockingbirds (Mimidae)	*Mimus saturninus*		1		
Thrushes (Turdidae)	*Platycichla flavipes*		3	3	
Blackbirds (Icteridae)	*Molothrus bonariensis*				11
	Ostinops decumanus		1		
Tanagers (Thraupidae)	*Tanagra chalybea*		1		
	Thraupis ornata		2	2	
	Habia rubica		1		
	Trichothraupis melanops		1		
	Thlypopsis sordida		1		
	Schistochlamys ruficapillus		1		
Sparrows, Finches (Fringillidae)	*Haplospiza unicolor*			4	

cubation behavior, but the few species for which data are available are mentioned below.

Absence of the patch in the two tinamou specimens (both female) agrees with the conclusion (drawn from field observations by earlier workers) that only the male incubates the eggs in this family. Presence of the patch in both sexes of the cuckoo *Guira guira* agrees with the observed fact that both sexes incubate. The presence of a patch in the one specimen (with fully active testes) of the Swallow-tailed Hummingbird (*Eupetomena macroura*) is surprising and requires confirmation; however, Robert T. Moore (1939:315—also in Bent, 1940:471) reports: "In Ecuador I have observed the male and female [of *Colibri cyanotus*, the Violet-eared Hummingbird] take turns incubating at the same nest and collected both sexes to substantiate this observation." The patch is presumably present in all females of the Dendrocolaptidae, Furnariidae, and Formicariidae, but breeding females were collected for only six species in these families. Two specimens, male and female, of the cotinga *Tityra cayana* showed the patch; both had been observed to incubate. The male of the related *Procnias nudicollis* has not been observed to incubate, and in the two males collected, the patch was absent. The presence of the patch in the females of the Tyrannidae is expected, but its presence in males of three species (*Myiodynastes solitarius*, *Empidonax euleri*, and *Phyllomyias griseocapilla*) is noteworthy. The absence of the patch in all 11 female specimens of the Shiny Cowbird (*Molothrus bonariensis*) is, of course, to be expected because of the parasitic habits of the species.

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BIRD DISTRIBUTION AND ECOLOGICAL CONCEPTS

A SYMPOSIUM DIRECTED BY V. E. SHELFORD [1]

PART I

THE CONCEPT OF THE BIOME AS APPLIED TO THE DISTRIBUTION OF NORTH AMERICAN BIRDS

BY EUGENE P. ODUM

IN discussing such broad topics as the relation of bird distribution to ecological concepts, one can easily become entangled in an effort to follow the various lines of thought suggested by the observable facts. In this, the introductory paper of the symposium, I shall therefore attempt to clarify and simplify rather than elaborate, presenting first a simple comparison of the life zone and biome theories, and second, a discussion of the theoretical and practical aspects of the biome concept as applied to the distribution of birds during the breeding season in North America. Since there are a number of recently published papers to which the reader may refer for definitions, details, and further explanations, I believe that I can best present my material in semi-outline form.

Classification by Community or Environment

Ecologists are often accused of creating a hierarchy of terms or systems of classification and then trying to fit all situations to them; hence it may be well to say a few words in justification of setting up systems for ecological classification even when knowledge is still in a formative state. From the time of John Ray and Linnaeus, the need for an orderly system of naming organisms has been universally recognized. But organisms do not occur in nature in such taxonomic groupings nor do they exist independently of one another; hence it is logical, as well as important, to study and classify them by their natural groupings (i.e., by actual communities). However, distributional classification is not an end in itself any more than taxonomy is. It is merely a useful tool in research; a method of organizing the manifold detail of field observations; a specific means of stimulating and directing research; an aid in orienting the student of distribution.

A new theory always stimulates investigation, but progress seems to be even more rapid when an opposing viewpoint is also presented. Witness the tremendous impetus given to biological study by the epigenesis *vs.* preformation and the evolution *vs.* non-evolution controversies. Work on classification by communities or environment has led to two important theories of distribution: Merriam's life zone system and the

[1] Presented before the Wilson Ornithological Club at Urbana, Illinois, November 21, 1941. Parts 2 to 5, by John W. Aldrich, J. J. Hickey, O. A. Stevens, and Roger Tory Peterson, and Part 6, a critical summary by V. E. Shelford, will appear in a later issue of the *Bulletin*.—Ed.

more recent biome system.[2] Discussions of these two theories have provided and undoubtedly will continue to provide a growing incentive for the study of the ecological aspects of distribution.

The Life Zone Theory

History. "Life zone," as a term, is too well known to ornithologists to require explanation. The life zone system was developed by C. Hart Merriam between 1890 and 1895 after he had observed the sharp "zonation" of life on San Francisco Mountain, Arizona. Impressed with the importance of temperature as a determinant, he formulated two temperature laws (Merriam, 1894:236) and mapped six zones as transcontinental bands along temperature isotherms (Merriam, 1898: map). Under Merriam's dynamic guidance, the life zone concepts had an important unifying influence on the pioneer field work of the U. S. Biological Survey and on the work of ornithologists generally.

Theoretical basis. Although temperature, which Merriam used as the basis (limiting factor) of his life zones, has proved time and again to be important, his temperature laws have not proved in practice an adequate basis for setting up major divisions of plant and animal life. Obviously, the actual distribution of organisms must serve as the basis of any logical, useful division and is, in fact, the basis used in the more recent discussions and mappings. (Merriam's two temperature laws have been criticized in detail by Livingston and Shreve, 1921; Kendeigh, 1932; Shelford, 1932; and Daubenmire, 1938.)

Application to actual distribution. Most of the recent applications of life zones have been concerned with restricted areas such as a mountain range or a single state (political unit), rather than with the fauna of an entire zone or with the entire distribution of any one species. Boundaries and bird "indicators"[3] have been set up for each locality, usually without much attempt to relate the locality to the continental zone as a whole, and when applied in this way to local distribution problems, life zone terminology has proved convenient to ornithologists. However, efforts to correlate such local studies have shown that the ranges of bird species agree well with Merriam's Arctic and Canadian zone divisions, but poorly or not at all with the Hudsonian, Transition, Upper Austral and Lower Austral zones. The Transition, Upper and Lower Austral zones, particularly, are not natural biotic units because they cut from east to west across regions of widely differing vegetation and avifauna. Dice (1923:43–44) points out that the life zone theory is "founded on the belief that there are zones of life extending transversely across the continent of North America, in the south as well as in the north;" that "belts of life do occur in the northern part of North America and on mountains, yet the recognition of transcontinental zones

[2] I have not made a detailed critical study of a third system of distributional classification (by "biotic provinces") recently proposed by Dice (1943).

[3] Specific organisms indicating the presence of certain conditions.

of life in the southern part of the United States seems contrary to the facts of distribution." This is the criticism most often made against life zones (see Ruthven, 1920; Shelford, 1932; Daubenmire, 1938; Pitelka, 1941).

Many indicators (or species characteristic of a given zone), such as those listed by Chapman (1932:32–34), fail to fit even remotely the zones they are supposed to represent. Thus such wide-ranging species of "seral" [4], or developmental, habitat as the Mourning Dove, Meadowlark, Bobwhite, or Kingbird, can hardly be considered characteristic simply of the Transition zone; nor are the Tufted Titmouse, Cardinal, Carolina Wren, and others, which Chapman (p. 33) lists for the Upper Austral, any more characteristic of that zone than of the Lower Austral.

The longitudinal division of the austral zones (i.e., the Transition, Upper Austral, and Lower Austral) into humid and arid portions helps to correct the above-mentioned failings of the life zone system but is not altogether satisfactory, since these divisions are highly arbitrary from the standpoint of environments. Obviously, the diverse conditions east-west across the continent require a number of major longitudinal divisions.

The original life zone concept more or less ignored the vegetation as a primary factor on the theory that although climate controls both fauna and vegetation, it affects one independently of the other. An increasing tendency has been evident, however, to base life zones on the vegetation; thus, "Canadian zone" in the minds of most ornithologists means "northern coniferous zone," and it is obvious that the "botanical" term describes the area far better than the "political" term. Biotic factors in general (both faunal and floral) have received more and more emphasis in the modified life zone concept of today (see Brooks, 1940:252–253, for example). Grinnell (1928; 1943:194) divided life zones into "associations," and associations into "ecological niches." Both terms emphasize community rather than temperature alone, and such shifts in emphasis direct attention to the fact that the terminology of the life zone system needs to be redefined or to be replaced by a more descriptive one.

Advantages of the concept. In bird study, the life zone theory has certain obvious advantages over other theories; most important among these are: (1) familiarity through long use by ornithologists and mammalogists; (2) simplicity and convenience (bird students find the concepts and terminology easy to grasp); (3) conformity with the evolutionary viewpoint in that it emphasizes the importance of temperature (climate) as a barrier to the northward and southward (and altitudinal) spread of species and genera.

[4] A "sere" in biogeography is the complete cycle or "series of communities that follow one another on any given area of the earth's surface" (Carpenter, 1938:242), from initial barrenness to the final, "climax" formation (as, for example, coniferous forest).

The Biome Theory

History. The concept of an association of diverse, mutually dependent organisms in a natural ecological unit (biotic formation, or biome) has had a gradual development which began at least as far back as 1877 when Mobius used the term "biocenose" for such an association or community. The studies and writings of Clements (particularly his 1916 plant succession monograph and subsequent work) and the work of Shelford have given wide currency to the concept in North America. In other parts of the world, similar concepts have been found useful by other workers, for example, C. G. J. Peterson, in his work on marine communities; J. F. V. Phillips in his work in South Africa; Palmgren in Finland; and W. N. Beklemischev in Russia. A detailed history and discussion of the biome theory in general is given by Clements and Shelford (1939); Pitelka (1941) has studied the distribution of North American birds in relation to the major biomes.

Definition. Biomes may be defined as major biotic communities, that is, natural groups of organisms characterized by the occurrence of certain plants and animals which are *dominant* (in the ecological sense of "controlling" the group and habitat) and *influent* (that is, exerting an important influence on the group and habitat). Since plants are usually *dominant* in terrestrial habitats, biomes are largely determined by the vegetation, specifically by the "climatic climax" [5] vegetation, but also by the important (i.e., *influent*) animals. Hence a biome map is not simply a vegetation map. Vegetation provides the background, as it were, but the occurrence of certain animals actually determines the major divisions; for example, although the northern coniferous forest biome is made up of several distinct plant "associations," the area is given unity by certain plants and animals ("binding species") whose range extends through all of the associations (Shelford and Olson, 1935:375–378).

Comparison of Life Zones and Biomes

In the life zones and biomes of North America (compare Chapman, 1932: end paper map, with Pitelka, 1941: Figure 1) the most obvious differences are as follows: (1) For the transcontinental austral zones of the life zone system, the biome system substitutes a number of community centers (biomes) east to west across the continent. (2) In the life zone system there is but one "transition" zone, but biomes are separated by a number of areas of overlap, or transition, called *ecotones,*[6] whose width depends on the rapidity of change, which, in turn is often determined by the topography (for example, often a biome is on high ground, the adjoining one on low).

[5] "The community in which an area ultimately terminates" (Carpenter, 1938:58).

[6] One of the most interesting ecotones that I have visited is the aspen parkland region of western Canada, which is a "three-way" transition area. Not only do coniferous forest species and grassland species meet here, but the breeding ranges of a number of typical eastern deciduous forest species (for example, the Redstart and Rose-breasted Grosbeak) have westward extensions through this region (Lincoln, 1935:37).

But it is in their approach to distribution problems that the fundamental difference lies between the life zone theory, which emphasizes the effects of physical factors on species or other taxonomic groups, and the biome theory, which emphasizes the development and distribution of communities. In many areas (especially in mountainous regions), the boundaries of life zone and biome units coincide; and there life zone maps differ from biome maps only in the names of the areas, employing the geographical (political) terminology of that theory instead of the biotically descriptive names of the biome theory.

Bird Distribution and the Biome Concept

The biome theory does not minimize the effect of temperature as a limiting factor but it takes into account other features of climate and recognizes the direct importance of cover (shelter or habitat). The organisms themselves are used as indicators, on the assumption that they are collectively better "judges" of the conditions than any measuring device yet invented by man. In the final analysis, the arrangement of biomes and their sub-units gives about equal emphasis to climate and cover. They are not the only limiting factors, of course, but on a continent, they are assumed to be the most important for the majority of species. Let us examine these and other factors in order to see if this is a logical assumption, particularly in relation to birds.

Climate. The climate of any given area is of such undoubted importance in determining all the life forms that little need be said except to point out that such factors as rainfall, humidity, wind, and solar radiation, are important as well as temperature. The climax vegetation is probably the best indicator of the sum total of climate (Clements, 1920:63–64). A map of climaxes is a much better map of climates than is a map of any single climatic factor.

Cover (shelter or habitat). Not only is habitat all important in determining local distribution, but it is increasingly recognized as a major factor in limiting the overall range as well. Its importance is clearly shown by the spread of certain species into areas (formerly unoccupied by these species) after changes in vegetation (cover) have occurred there even without change in climate. One could list numerous recent examples of this, such as the spread of the Robin into the grasslands after the planting there of trees, the southward spread of the same species with "opening up" of forest and planting of lawns, the spread of Prairie Chickens into the coniferous forest area of Wisconsin after deforestation, or the eastward spread of the Prairie Horned Lark into extensive man-made grasslands in the eastern deciduous forest area. On the other hand, many other species fail to spread even when suitable habitat is available or made available; for example, the Wood Thrush, Eastern Wood Pewee, or Crested Flycatcher have not (as yet) spread into extensions of the original deciduous forest; in these cases climate (or

some factor other than cover) may be the major limiting factor. Thus, the activities of man that produce changes in cover without change in climate may enable us to determine which of the two factors is the more limiting for particular species. Otherwise because of our present lack of knowledge of basic physiological and psychological responses of birds, it is by no means easy to come to a conclusion on this point. For example, J. J. Murray (1940:57), who has given us some excellent observations on the zonal distribution of Virginia mountain birds, observes that the Yellow Warbler occurs commonly in the valleys but not in clearings or orchards at high altitudes. Murray concludes from this observation that habitat is not limiting in this instance, whereas I would draw the opposite conclusion for the following reasons: Since the Yellow Warbler breeds far to the north (to the limit of willows on the tundra's edge) there would be no reason to suspect that climatic conditions on even the highest mountains in Virginia would be too rigorous for this hardy species. Topography and habitat, on the other hand, would be definitely against the species since suitable breeding habitat at high altitudes in Virginia is very limited in area and isolated by extensive stretches of unsuitable habitat. If the clearings at high altitudes became more extensive and sufficiently connected with lower areas I would be willing to predict that the Yellow Warbler would eventually invade them. The extent and position of apparently suitable habitat must be taken into consideration. In the other examples (tanagers, Veery) listed by Murray in the same paragraph, the evidence for climatic limitation is much clearer, but even in these, community factors cannot be ruled out completely.

Physiographic barriers. Though a primary consideration in limiting an island group, physiographic barriers in a large continuous land mass such as North America are obviously of less importance (as compared with habitat and climatic barriers) so far as distribution of birds is concerned. Physical barriers are, of course, indirect determinants of biomes since they greatly affect climate and vegetation.

Food. Although very important in determining the local distribution and abundance of birds, food rarely seems to determine the actual range of a species. The periodic fluctuations in populations of small mammals, for example, definitely affects the abundance and breeding of tundra hawks and owls, but since such mammal food is available in virtually all regions, its occurrence on the tundra is probably not a factor in restricting the range of tundra bird species. In other words, it is the exception rather than the rule to find correlation of the range of a bird species with the range of a specific kind of prey as, for example, the ranges of the Everglade Kite and Limpkin (J. B. May, 1935:18; Harper, 1936) seem to be correlated with the distribution of the snail *Pomacea* (*"Ampullaria"*).

Biotic interactions (*coactions*). The role which competition and predation play in limiting ranges is not yet well understood. It is of undoubted local importance just as food is, and may be a factor in limiting the spread of some species. We need to know more about the alleged limiting relations between such pairs of species as the Whip-poor-will and Chuck-will's-widow, the Bewick's Wren and House Wren (see, for example, E. V. Miller, 1941:84).

"Life form" of plant vs. *species of plant*. In general, few species of birds are restricted to a particular species of plant, but many birds seem to be limited to a particular type ("life form") of vegetation. For example, many species have a distinct preference for coniferous forest, but it may not make much difference whether it be spruce, fir, or hemlock. Thicket birds select bushy growths of a specific density rather than of a particular shrub species. Grassland birds may be equally at home in beard grass, mesquite grass, or bluegrass, if the stands are of the same general density or appearance. As Grinnell (1943:183) once remarked, "the presence of a certain kind of perch or particular sort of forage surface is practically essential to the presence of a given kind of bird whose structures and instincts are adapted to it." More adequate means of measuring the importance of this "structural" feature of the vegetation are greatly needed. Many species are very adaptable to changing *species* of vegetation (for example, when cultivated grasses replace native prairie grasses—Bennett and Hendrickson, 1939), but are unable to adapt to a new *life form* or even to small changes in habitat *structure*. Within a biome, it is the *life form* of the climax vegetation that tends to be uniform rather than the *species* of the dominant plants.

Conclusion. Considerable study may be necessary to determine the critical limiting factors for individual species. For "stenothermic" species (species with limited climatic tolerance), climate will prove to be limiting at least somewhere around the range boundary; for species with wide climatic tolerance (like the Robin), habitat or other factors may be limiting. In general, however, climate and habitat seem the most important. Therefore, a classification system (such as the biome theory) that considers both these major factors, as well as intra-community relations in general, is bound to produce a better correlation of its divisional units with the distribution of a larger number of species than a system based on one factor alone.

Evaluation of Biomes

Climax and seral communities. It is important to distinguish between *climax* and *seral* (developmental) communities since bird distribution is greatly influenced by the dynamic nature of succession.

"The last community of . . . a succession is the *climax* which is self-perpetuating and is characterized by a life-form of the dominants, such as grass, deciduous forest, etc. The dominants of developmental stages within a climax region may or may not be of the same life form, as, for example, seral stages in the deciduous forest climax may include herbs, grasses, shrubs, and both coniferous and deciduous trees" (Pitelka, 1941:115; see also Weaver and Clements, 1938: chap. 3).

Thus the habitat of early seral stages is often very different from that of the climax, with corresponding differences in avifauna. These differences ***within*** a biome should not be confused with differences ***between*** biomes.

When the climaxes of different biomes are compared, each is seen to have a very characteristic group of birds. Comparatively few species occur in the climax of more than one biome—which helps give the biome its identity as a natural community. Not all climax species, of course, have ranges that exactly correspond with the biome. When a species does not occupy all its biome, or when it spreads to other biomes, the ecologist's attention is focussed on the special factors limiting that particular species, just as a "difficult" genus stimulates the work of the taxonomist.

It is not uncommon for a species to occupy the climax of one biome and the seral (developmental) stages of one or more others. The Red-eyed Vireo, for example, occurs abundantly in three biomes, but occupies the climax only in the eastern deciduous forest biome, being restricted in the coniferous forest biome to developmental communities (e.g., aspen) and in the grassland biome, to "colonies" of sub-climax forest (e.g., streamside forests).

The most widely distributed species such as the Song Sparrow, Yellow Warbler, Mourning Dove, Red-wing, and various water birds, breed in the early developmental stages of vegetation. The early developmental stages (unlike the climaxes) of widely different regions often have a similar appearance and thus offer suitable habitat for species with wide climatic tolerance. A marsh, for example, provides much the same sort of habitat in various biomes. We would expect, therefore, that "seral" birds would show less correlation with biomes than "climax" birds do; but while this is generally true, many early seral birds are restricted to certain biomes or sub-regions, the climatic (or "non-habitat") features of the community apparently holding them there.

Primitive vs. *disturbed conditions*. It is important to distinguish between primitive, or natural, conditions (by which ecological units are delimited) and disturbed conditions directly or indirectly produced by man.

Man has perhaps changed the climate little, but he has greatly modified shelter, food supply, and other "habitat" factors. Man tends

to produce a forest edge condition wherever he settles, whether in forest or grassland, that is, he thins the forest, creating openings, or, in grassland, plants trees. In general, he increases greatly the areas occupied by seral vegetation at the expense of the climax areas. The sharp natural differences between regions are thus reduced, and "forest edge" species with wide climatic tolerance are encouraged to spread. Thus, lists of *roadside* and *farmland* birds which we compiled on a 6,000-mile trip through western North America were monotonously the same regardless of the biome (or life zone) traversed, whereas birds of *natural* communities were excitingly different from biome to biome.

Man's indirect influence is, of course, felt far from his habitations. Lumbering (plus forest fire) and overgrazing have produced extensive fundamental changes both in vegetation and bird populations. In the central Alleghenies the effect of such changes on breeding warblers has been carefully analyzed by Brooks (1940); in Manitoba one sees aspen forests and Red-eyed Vireos over a wide area where (to judge from the prevalence of charred spruce stumps) spruce and warblers once were; in some places, destruction of the climax vegetation is so complete that the forest may, for lack of seed trees, never be restored; likewise, huge areas of western Texas, New Mexico, and Colorado that once were grassland are now sage brush or mesquite desert. Such alterations produced and maintained by man and domesticated animals are often called "disclimaxes" and should not be confused with the true or potential climax, which is determined by climate.

Man, of course, *directly* modifies the distribution of a few birds through the introduction of exotic forms, "control" by direct predation (hunting, destruction of "undesirable" species, etc.), and through wildlife management.

Biomes are based on the primitive or potential conditions. This is not only convenient, but provides the point of reference for evaluating man's influence on his environment. Thus, preservation of primitive areas is desirable not only from the esthetic point of view but from the practical one as well, and ecologists and ornithologists should make every effort to study such natural areas in order to determine how far man has already changed conditions and how far he may change them without disastrous results.

Lack of quantitative data. In studying the correlation between distribution of species and natural areas, the lack of quantitative data is a great handicap (Pitelka, 1941:116–117). The usual check-list notations and most maps so far published are not very helpful since they indicate only the extremes of a given bird's range and fail to show where the species is really a common and influent member of a community. It would help greatly if, in describing abundance and habitat, compilers

of local lists would give at least as much attention to common species as they currently give to rare ones.

Distribution of subspecies. So far in the discussion, we have considered only the distribution of full species (including, in the case of multiform, or polytypic, species, all of the subspecies). Little can be said regarding the occurrence of subspecies in relation to biomes, not only because they have not been studied from this angle, but also because the criteria used to delimit subspecies are variable, and lines drawn between races must in many cases be more or less arbitrary. As monographic studies, such as that of A. H. Miller (1938) on the Junco, have abundantly shown, morphological characters of subspecies do not "change simultaneously geographically" in transition from one extreme form of a series to the other; color, body size, length of bill, and other characters may all vary geographically although independently of one another. Nevertheless, geographical variations in bird forms are undoubtedly correlated with environmental complexes, and taxonomists should give more consideration to natural community units when dividing a species into races. Aldrich and Friedmann (1943) have recently made an admirable attempt to correlate subspecies of the Ruffed Grouse with biotic communities. Paralleling and supporting this particular emphasis (as well as the general emphasis that the biome theory gives to biotic factors) is the change in the basic concept of species, which is becoming broadly biological rather than strictly morphological (see Mayr, 1943: chap. 5 and 6).

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GENERAL NOTES

Soaring geese at Tulelake, California.— At 1:10 P.M., February 27, 1944, while making observations on birds at the Tulelake National Wildlife Refuge, Tulelake, California, I heard the calling of a flock of Snow Geese (*Chen hyperborea*) as it passed rather high overhead. Noting that their flight was somewhat different from normal, I examined them through field glasses. The entire flock of 22 Snow Geese was clearly riding with outstretched set wings what was evidently a rising current of air. Their soaring was much like that of the Little Brown Crane (*Grus c. canadensis*) and Sandhill Crane (*G. c. tabida*) which I have watched in eastern New Mexico under similar weather conditions. I watched the flock of Snow Geese for more than 10 minutes as it drifted northward. During that time, I noted only an occasional wing beat. Shortly after the flock passed, a flock of 12 White-fronted Geese (*Anser albifrons*) passed, employing the same flight tactics. Their flight was also in a northerly direction. At the time of the observations the day was clear and warm, with only a slight breeze from the north. The soaring of these geese was evidently similar to that reported by Williams (*Condor*, 44, 1942:76) near Brigham City, Utah, in the fall of 1941. —CLARENCE A. SOOTER, *U. S. Fish and Wildlife Service, Alice, Texas.*

Reaction of American Mergansers to Herring Gull depredations.—On February 16, 1943, Burt L. Monroe, Thomas Smith, and I observed the following episode, which illustrates some aspects of bird psychology. A flock of 12 to 15 Herring Gulls (*Larus argentatus*) and 8 American Mergansers (*Mergus merganser americanus*) were fishing eight miles east of Louisville, Kentucky, at the mouth of Harrod's Creek. The small creek had frozen to within a hundred yards of its mouth, but the bay and river were open. We drove close to the shore and remained partially concealed in our automobile behind a large tree.

Soon a male merganser after a deep dive came up with a large fish in its bill. Instantly five or six of the gulls took wing and converged on the duck. The nearest gull easily snatched the fish, but being unable to swallow so large a mouthful soon lost it to another gull. The other gulls fought for possession until the fish was torn to bits. This happened several times, with the result that the mergansers were losing most of their catch. (With the broad expanse of the Ohio River, which was here more than 1,000 yards wide, to choose from, the mergansers remained to endure the persecution of the gulls probably because of the superior fishing at the mouth of the frozen creek.)

After a while, we noticed a gradual change in the fishing tactics of the mergansers. One came up with a fish. As usual, several gulls went for it, but before they could snatch it, the merganser dived with the fish still in its mouth. He came up 20 feet away in an open space and while swimming as rapidly as possible swallowed the food before the gulls could reach him. One gull, swooping too late for the fish, struck the merganser with all its weight, causing him to bob up and down, yet not frightening him enough to make him fly. Other mergansers also developed a watchfulness which enabled them to retain more and more of their fish. They seemed to pick spots in which to surface as remote as possible from the gulls, and they swallowed their catch quickly while avoiding the attacks of the gulls by swimming or diving.

After failing repeatedly to rob the mergansers of their fish, the gulls gradually lost interest and drifted farther out from shore, allowing the mergansers to fish unmolested. The ability of the American Mergansers to modify their behavior successfully in the face of the depredations of the gulls shows a surprising degree of adaptability.—HARVEY B. LOVELL, *Biology Department, University of Louisville, Louisville, Kentucky.*

Migration records from Yucatan.—The following selected observations, recorded along the north coast of Yucatan chiefly during the spring months of 1936, may prove of value in connection with the recent discussions of trans-Gulf migration. In each instance reported, both the behavior of the birds and the attendant circumstances suggested that the birds were en route across the Gulf.

Turkey Vulture. Between February 2, and March 25, 1936, only one to six Turkey Vultures (*Cathartes aura*) were recorded in the vicinity of Chichen Itza in the central part of the Yucatan Peninsula, some 50 miles inland from the north coast. On March 26, a flock of 13, and on March 27, individuals and small groups totaling 15, were moving northward over Chichen Itza. On March 31 and April 1, three to five separate individuals left the Yucatan shore between Progreso and Chicxulub (east of Progreso) and flew northward over the ocean until out of sight. About 8:00 A.M., April 2, a flock of seven came from the south and continued northward over the Gulf. In the clear atmosphere the large birds were visible for a great distance. On the same day, several individuals and small groups, totaling 18 birds, flew northward across the highway between Progreso and Chichen Itza.

Sparrow Hawk. On the morning of April 7, 1936, two Sparrow Hawks (*Falco sparverius*) were perched on the beach near Progreso within a few feet of the water. They repeatedly flew out over the Gulf but returned to the beach or to the vegetation immediately behind it. Finally, about 10:00 A.M., one of the hawks left the beach and flew northward over the ocean until lost from view.

Sandpipers. On March 31, 1936, many sandpipers were about the mud flats at Progreso. About 60 were identified as Least Sandpipers (*Erolia minutilla*), about 80 as Semi-palmated Sandpipers (*Ereuntes pusillus*). At dusk, several small compact flocks of "peeps" left the flats and flew northward over the water until out of sight.

Hummingbirds. On April 1, 1936, there were numerous hummingbirds on the beach between Progreso and Chicxulub. Some were perched among the sparse vegetation of the dunes, some on the beach itself—a number at the water's edge. About 60 were identified as Ruby-throated Hummingbirds (*Archilochus colubris*). At intervals throughout the day, individuals and small groups left the beach and flew northward over the ocean. Some returned after flying a little distance, but others continued northward until out of sight, and by evening few remained on the beach.

Barn Swallow. On April 7, 1936, a flock of some 40 Barn Swallows (*Hirundo erythrogaster*) was feeding and flying about the front beach and adjacent sand dunes between Progreso and Chicxulub. At intervals the birds flew out to sea until almost out of range of 8 x binoculars, then returned to resume feeding. Each time they flew outward, they stopped the customary revolving movements of feeding birds and assumed a disc-shaped formation. Finally, at about 10:30 A.M., they assumed this formation and flew northward over the ocean until out of sight. At 8:30 A.M. on August 11, 1937, two Barn Swallows, one adult and one immature, were perched on the stern of the ship *Munplacé*, which was then some 80 miles north of Progreso and moving northward. The two birds remained about the ship all morning, alternately perching on the rail and making excursions over the water. Although it has been supposed that swallows, in particular, migrate around the Gulf, these were apparently early fall migrants en route south across the Gulf. If this assumption is correct, the record has additional interest in relation to the well-known theory that swallows migrate only during daylight hours, since part of the migration of these swallows would necessarily have taken place during darkness. Worthington and Todd (*Wils. Bull.*, 38, 1926:220) also cite an instance of apparent night migration of the Barn Swallow.

Wood warblers. Throughout each day, and occasionally during early evening, in the spring of 1936, small birds, warbler size and with the *chips* of warblers, flew northward across the beach near Progreso and continued over the ocean. Between 9:00 and 11:00 P.M. on March 30, there was an unusual number. It was brilliant moonlight, and the wind was in the north-northwest.—JOSSELYN VAN TYNE, *Ann Arbor, Michigan,* and MILTON B. TRAUTMAN, *Stone Laboratory, Put-in-Bay, Ohio.*

Record of the Turkey from the Pleistocene of Indiana.—In 1936 Mr. Alton Bernhardt of North Liberty, found part of the cranium of a *Cervalces* at a locality on the headwaters of the Kankakee River, Indiana (C. L. Gazin. *Amer. Midl. Nat.* 19, 1938:740, figs. 1–2). This specimen he presented to the United States National Museum through the late Marcus Ward Lyon, Jr. In the summer of 1938 Mr. Bernhardt again visited this site to look for further bones, and on this occasion found the left humerus of a Turkey (*Meleagris gallopavo*) that he has also kindly given to the National Museum. The specimen, while of good size, comes from an immature individual in which the bone is not yet fully formed. The locality is along a drainage ditch near Potato Creek, a mile east and about three-quarters of a mile north of North Liberty, St. Joseph County. The turkey humerus was secured about 20 feet from the point where the *Cervalces* skull was collected. This is the first record for this species for the Pleistocene of Indiana.—ALEXANDER WETMORE, *Smithsonian Institution, Washington, D.C.*

Gulls and terns hawking flying insects.—A note by Milton and Mary Trautman on Ring-billed Gulls fly-catching (*Wils. Bull.*, 57, 1945:77) reminded me of my own observations along those lines in recent years, and the following extracts from my diary may be worth adding to the record. On September 2, 1943, while travelling from Fort Erie to Niagara Falls, Ontario, along the Niagara River boulevard, I saw great numbers of birds, obviously feeding on insects, hovering and darting high in the air over the road and inland across the fields almost as far as the eye could see. The insect eaters were nearly all terns and gulls, with Black Terns (*Chlidonias nigra*) in various plumage phases very much in the majority. However, Ring-billed Gulls (*Larus delawarensis*) were also well represented, and some near by were plainly seen to be snapping up the flying insects in an efficient if somewhat awkward manner. A few Bonaparte's Gulls (*Larus philadelphia*) were similarly engaged, and one or two Nighthawks (*Chordeiles minor*), with lighter and more airy flight, and apparently much greater skill, were joining in the feast. Common Terns (*Sterna hirundo*), in great numbers over the river, were busy diving for fish, but once in a while a Common Tern would join the insect hawkers when a group of them happened to come close to the river bank. A few miles further down the river, toward Chippawa, other insect hawking flocks of gulls and terns were encountered; one fairly large group was predominately Ring-billed Gulls, while a smaller group, still nearer Chippawa, was largely composed of Black Terns. About a year later, on September 13, 1944, at several points along the river boulevard, from Old Fort Erie to near the mouth of Black Creek, Ring-billed and Bonaparte's Gulls in considerable numbers were observed hawking insects. The insects were not certainly identified, but at Fort Erie they seemed to be chiefly caddis flies, and near Black Creek, either caddis flies or flying ants. At Fort Erie, almost 50 per cent of the hawking gulls were Bonaparte's, but lower down on the river, the insect-eating flocks appeared to be composed almost entirely of Ring-billed Gulls. On both of the occasions cited, flights of ants were general throughout the area. Those on which the gulls and terns were apparently feeding seemed to be largely referable to the genus *Lasius*.—R. W. SHEPPARD, *1805 Mouland Avenue, Niagara Falls, Ontario.*

EDITORIAL

Unfortunately, the meeting of the Wilson Ornithological Club Council which was scheduled for August 20 had to be canceled. Arrangements for a later meeting have not yet been completed.

The following Nominating Committee has been appointed by President Kendeigh to prepare a slate of Wilson Ornithological Club officers and Council members for 1946: Ernst Mayr, Chairman; W. J. Breckenridge; Ralph E. Yeatter. They will be glad to receive suggestions from members of the Club.

We wish to thank our loyal Life Member, Bernard W. Baker, for the generous gift which makes it possible to publish in color his handsome photograph of the Prairie Warbler that illustrates this issue.

OBITUARY

George Willett, ornithologist of the Los Angeles Museum and Vice-President of the American Ornithologists' Union, died August 2, 1945, at the age of sixty-six. His very extensive field experience in Alaska and California was the basis for many valuable reports, including detailed studies of the avifauna of southwestern California.

Ornithological News

The concluding part of H. Kirke Swann's "Monograph of the Birds of Prey" has just appeared. The first part was published in 1924, but Swann died in 1926 when only five additional parts had been printed. Alexander Wetmore generously agreed to undertake the completion of his friend's work, and publication was resumed. Many unforeseen difficulties had been overcome, and the concluding part was finally on the presses in September 1940, when German air raids completely destroyed the London printing establishment. Fortunately, the publishers, Wheldon and Wesley, had a set of corrected proofs stored outside London, and the text was gradually reset from this copy as war-time conditions permitted. Further delays resulted when new proofs, in transit between England and America, were twice lost at sea from enemy action. The completed work stands as a monument, not only to H. Kirke Swann, but to the courage and persistence of Alexander Wetmore and the publishers.

Jean Delacour and Ernst Mayr have completed for publication a manual of the birds of the Philippine Islands. The book is illustrated by Alexander Seidel and Earle L. Poole.

W. E. Clyde Todd and J. K. Doutt of Carnegie Museum spent the spring and summer studying the birds and mammals of the tundra country on the east coast of Hudson Bay, north of Lake Minto.

William Beebe has just returned from six months' study of birds and other animals at the field station of the New York Zoological Society at Rancho Grande, Maracay, Venezuela.

Ralph Ellis has moved to Lawrence, Kansas, and has lent his remarkable ornithological library to the University of Kansas Museum of Natural History. The library (some 65,000 volumes) is perhaps the largest private collection of books on birds and mammals in the world. It includes some extremely valuable manuscripts, as well as sets of the original sketches and drawings of famous artists. Of particular interest are the large number of sketches by John Gould and 650 drawings of the birds of India by Thomas C. Jerdon.

ORNITHOLOGICAL LITERATURE

CHECK-LIST OF BIRDS OF THE WORLD, Vol. 5. By James Lee Peters. Harvard University Press, Cambridge, Mass., 1945: 6 x 9 in., xi + 306 pp. $5.00.

The publication of another volume of Peters' Check-list, which now covers 92 families, 1,009 genera, 3,344 species, and 8,007 subspecies of birds, is news of the first importance to ornithologists everywhere.

This new volume fully maintains the very high scholarly standard set in the earlier parts; it even exceeds them in fullness of treatment, detail of synonymy, and number of helpful annotations. Only the physical make-up of this volume has suffered; war-time conditions have forced the use of a poorer, less opaque, paper and the elimination of the protective gilt top.

Peters gives us no statistical recapitulation of his results, but because such a summary is of general interest and real biological importance, a tabulation of the numbers in each category under the twelve families treated in this volume is given below.

	Genera	Species	Subspecies
Trochilidae, Hummingbirds	123	327	688
Coliidae, Colies	1	6	29
Trogonidae, Trogons	8	34	103
Alcedinidae, Kingfishers	14	87	337
Todidae, Todies	1	5	5
Momotidae, Motmots	6	8	45
Meropidae, Bee-eaters	7	24	50
Leptosomatidae, Ground-rollers	1	1	3
Coraciidae, Rollers	5	16	37
Upupidae, Hoopoes	1	1	9
Phoeniculidae, Wood-hoopoes	2	6	27
Bucerotidae, Hornbills	12	46	104
TOTALS	171	561	1437

Peters has listed the Leptosomatidae first in the suborder Coracii, but otherwise follows exactly Wetmore's (1940) arrangement. Five new names are proposed in this volume, but they represent mere changes in "labels" applied to already known biological entities.

Only a few of the other changes proposed relate to birds of the area covered by the A.O.U. Check-List. Rivoli's Hummingbird, of Arizona, is listed as *Eugenes fulgens fulgens* (not *E. f. aureoviridis*, as in the Nineteenth Supplement); Salvin's Hummingbird (*Amazilia salvini*) is dropped, since it is believed to be only a hybrid; the Calliope Hummingbird becomes *Stellula c. calliope;* the Copper-tailed Trogon is represented by one subspecies (*Trogon elegans canescens*) in Arizona and by another (*T. e. ambiguus*) in "extreme southern Texas"; the Belted Kingfisher is again placed in the genus *Ceryle*.

More than half of the volume is devoted to the hummingbirds—a family that has always attracted the special attention of ornithologists and nevertheless still baffles their best attempts at classification. In the introduction, Peters makes it quite clear that he is far from satisfied with his own results, and he even suggests that the next reviser should attempt a classification based on the females, since the present arrangement over-emphasizes the secondary sexual characters of the male.

Although Peters remarks that generic differentiation has been much over-done in the Trochilidae, his own classification does little to remedy that fault. He has indeed reduced to subgeneric status several groups hitherto given full generic rank, but he ends by recognizing five more genera than did Sharpe in 1900, although

only four new hummingbirds requiring generic recognition have been discovered since that time. Almost half of the genera he lists are monotypic.

It is interesting to compare the numbers of genera, species, and subspecies recognized by the last four ornithologists to revise the hummingbirds:

Sharpe (1900): 118 genera, 570 forms;
Cory (1918): 130 genera, 649 forms;
Simon (1921): 189 genera, 660 forms;
Peters (1945): 123 genera, 688 forms.

Hummingbirds exceed most other bird groups in their propensity to hybridize, and many of Peters' notes deal with this remarkable characteristic. It will be a long time before our lagging knowledge of live hummingbirds reaches a point where we understand the nature of this phenomenon and its psychological and physiological causes.

Our extraordinary ignorance of hummingbirds is strikingly demonstrated again and again. For example: two genera and nine additional species have never been seen in life by any ornithologist but are based solely on Bogotá trade skins; many others are represented by only one or two specimens and are therefore almost equally unknown as living animals.

Peters' well-balanced judgment and careful attention to every detail are evident throughout the book. He has again given us a first-class piece of work, and we wish him all speed in his great undertaking, which so immeasurably stimulates and facilitates ornithological research.—J. Van Tyne.

THE DISTRIBUTION OF THE BIRDS OF CALIFORNIA. By Joseph Grinnell and Alden H. Miller. Cooper Ornithological Club, Pacific Coast Avifauna No. 27, Dec. 30, 1944: 608 pp., 1 col. pl., 57 figs. $6.00 (cloth, $7.00).

Almost every year sees one or more additions to the literature on local, state and regional avifaunas. They are all useful to the growing corps of bird students; some are briefly annotated check-lists; others are well-illustrated volumes with keys, descriptions, and much textual matter on habits. Nearly all have one characteristic in common: their object is to tell the reader what birds occur or have occurred in the area in question, in what numbers, and at what times of the year. They are geographic studies, with little or no systematic or taxonomic investigation; the A.O.U. Check-List and its supplements are accepted.

A combination of circumstances makes the present list a much greater enterprise. The very large state of California has great diversity of terrain and climate, caused by numerous mountain systems. The degree of subspecific variation is not exceeded in any other part of the continent. Drs. Grinnell and Miller, as life-long students of these variations, with ample field experience, and the best regional collections in the country, have every right to express their judgment on many knotty and controversial racial problems. They are to be commended for not hesitating to depart from the taxonomy of the A.O.U. Check-List. Indeed, it would have been most unfortunate if their knowledge, opinions, and experience had been "put to sleep," as it were, in slavishly following a check-list printed in 1931. The reader, however, is cautioned against concluding that either the authors or I disbelieve in the general usefulness of a check-list prepared by a committee. The committee has undertaken an arduous and protracted labor in the hope of producing a useful general reference work, without claiming that everything is settled, and further research superfluous or impertinent. Such assumptions are too easily made by the ignorant or ill natured, who are not competent to judge whether, for example, the Black Petrel should be in a special genus, *Loomelania*, or not. But Dr. Miller has every right to believe in the validity of *Loomelania* and publish his reasons, even if to date a majority of the Check-list Committee do not. It gives me particular pleasure to defend this right, because I do not happen to think *Loomelania* necessary myself!

It follows from all this that years of systematic study underlie a work purporting from its title to be distributional. Indeed, it entailed a review of most of the birds of western North America. It also entailed a careful consideration of vernacular or "common" names. Dr. Miller does not believe in vernacular names for subspecies, but admits that this unfortunate practise has got too firm a start to be discontinued now. He has done the next best thing and devised a logical system. Every species has a name, and every subspecies of that species has a name which *clearly shows* its specific affinities. Bailey's Chickadee becomes Bailey's Mountain Chickadee. The typical subspecies also has a subspecific name. The term "Pygmy Nuthatch" is used for the species *Sitta pygmaea* as a whole; *Sitta pygmaea pygmaea* is the "Monterey Pygmy Nuthatch," not the "Pygmy Nuthatch," as in the A.O.U. Check-List. Common names are altered from person's to geographic names, whenever a short term is possible and obviously of greater meaning and more readily memorized. The subspecies of the Chestnut-backed Chickadee are quite changed around. The Chestnut-backed Chickadee of the Check-list (typical *rufescens*) becomes the Northern Chestnut-backed Chickadee, expressing the facts of its geographic range; the Nicasio Chickadee becomes the Marin Chestnut-backed Chickadee, because the county is less local than the town which happened to be the type-locality; Barlow's Chickadee becomes the Santa Cruz Chestnut-backed Chickadee, after the faunal area in which it occurs. Dr. Miller, therefore, has generally agreed with numerous recommendations along these lines, and has put them into execution. He is not so pedantic as to believe that vernacular names have a fixed code of nomenclature, which is forced to apply an imaginary law of priority in every case.

We can now consider the methods adopted in outlining the distribution of the 644 native species and subspecies admitted to the state list. Each taxonomic entity is discussed under four headings. (1) A very brief synonymy is confined to other scientific or popular names under which California records for the species in question have been published. (2) A paragraph on status is particularly commendable for summarizing any increase or decrease in range or numbers and the probable reason therefor. (3) A long paragraph on geographic range in California (in most cases very detailed) with dates of notable records and the references. In all cases where a species involves several subspecies, intermediate populations and others of doubtful status are outlined. Every effort is made to bring out all cases where something is not definitely known or settled about California birds, and the authors are far more interested in those birds normally an integral part of the California avifauna than in waifs, strays, vagrants, and accidental stragglers. (4) A final paragraph on habitat is a particularly valuable feature. It avoids any stereotyped formula or system; the preferred plant association or ecological niche is described first. The authors, happily, are slaves neither of the biome or the life-zone theories of distribution.

One of the most controversial elements in any state or local list is the basis the authors select for the inclusion of species in the list. *No* system is free from attack; in any case some people will be disappointed or offended; some arbitrary standard *must be* adopted, and the inclusion or exclusion of certain species will appear unreasonable or absurd. The larger the area and the more species involved, the more cases are bound to arise which will teeter, so to speak, on the hairline of rejection or acceptance, *no matter what criterion* is adopted. Our authors have chosen to include no species for which no specimen is extant as a voucher, which means the rejection of some species seen a number of times, in some cases of very distinctive appearance in life, such as the Reddish Egret, Little Green Kingfisher, and Canada Warbler. The only exception, open of course to attack, is the inclusion of certain stragglers, where the bird was caught in a banding trap and handled in the flesh. While not ordinarily regarded as open to attack, sight records of other stragglers are given as official records, provided that somebody

else shot a specimen, though no one has ever satisfactorily explained how A's sight record is validated by B's specimen obtained somewhere else another year! Students of birds are earnestly begged to reflect on the following facts. (1) The more scientific the study, the more proof is required. (2) The more scientific the study, the less interest and importance attaches to the casual or accidental. (3) The more thorough and scientific the review of a great and diversified continental area with a rich and varied bird-life, and the more decades of research and study preceding the review, the more errors appear in records *based on specimens*. There is nothing sacrosanct about a specimen. All one has to do is to turn to the supplementary list of the present work (pp. 557–576). Eleven species are excluded because the records are sight records only. *Thirteen* species are excluded, because the original specimens are no longer extant, and *37* species are excluded in spite of existing specimens, because the specimens were misidentified, erroneously ascribed to California, represented possible escapes from captivity, or for similar reasons. No one, therefore, can claim that Dr. Miller is "picking on" the opera-glass student. He has also "picked on" a fair percentage of the world's leading ornithologists of the past 80 years! They either made mistakes or were more credulous than he. Finally, (4) no count is possible of the innumerable cases where specimens formerly referred to one subspecies are now referred to another.

I am convinced that the only way to end the absurdities of vernacular names for subspecies and to discourage amateur observers from using them is to eliminate them. I am equally convinced that the only way to discourage the amateur observers' worship of the rare vagrant is to take *all of them* out of the main body of every state list and put them into an appendix with the curtest possible mention. Scientifically, it makes little difference whether a vagrant has occurred once or five times; the year and place of capture are of little consequence; and even the month is abnormal or else within the known period of migration.

Pacific Coast Avifauna No. 27, is one of the most scholarly regional studies of North American birds ever published. It is calm and temperate scholarship, the underlying principles are well formulated in an introduction which should be read by every American ornithologist contemplating a similar work. Dr. Miller did half of it alone after Dr. Grinnell's death in 1939, and brought the first half up to date. But "we" and "our opinion" occur throughout the book, proving that Dr. Miller is a loyal gentleman as well as a scholar.—Ludlow Griscom.

BIRDS OF GEORGIA. By Earle R. Greene, William W. Griffin, Eugene P. Odum, Herbert L. Stoddard, Ivan R. Tomkins, and Eugene E. Murphey. *Georgia Ornith. Soc. Occ. Paper No.* 2. Univ. Georgia Press, Athens, 1945: 6×9 in., 111 pp., 1 pl., 1 map. $2.00.

Few southern states are fortunate enough to have up-to-date, comprehensive publications on their avifauna, and there are even comparatively few local lists for southern regions. This accounts to a certain extent for the vague and sometimes erroneous statements on distribution in the last A.O.U. Check-List (1931) and in other publications of broad geographical scope. Before the appearance of the present volume there was no single publication listing all of the species of birds known to occur in Georgia. Consequently "Birds of Georgia" is welcomed as a notable contribution to the ornithology both of the state and of the South as a whole. The compilers make no pretense of their work being complete but express the hope that the volume "will provide both a sound basis for future publications and a stimulus for research in the field."

Excellent judgment has been shown in deciding which species to admit to the list and which to reject because of insufficient evidence. Even records by Audubon that do not include definite dates and specific localities have been rejected. Except in a very few instances of records relating to large and easily

recognizable birds, a preserved specimen of a form is considered by the authors the primary requisite for inclusion of the form in the list. It would be well for all ornithologists, particularly compilers of check-lists and distributional synopses, to realize that in no other field of faunistic zoology are distributional records so often based on such "unprovable" data as sight records. Although the usefulness of sight records in determining frequency of occurrence, relative abundance, and type of habitat, is to be admitted, such records can rarely be accepted as real evidence of the occurrence of a species in a given region, are of questionable value in delineating accurately the range of a species, and are usually of no value whatever when they relate to subspecies. Certain works on the avifauna of the South require radical revision simply because the authors failed to scrutinize all records, to omit (or to admit only with clearly stated qualification) those about which there was any doubt, however small. Proof in science is never based on probabilities. Consequently, even if there is only the proverbial "one chance in a thousand" that a sight record of a given bird might apply to some other species (however remote the range of that other species), then the record is of little value, particularly if it constitutes the only record for the geographical area in question.

Hence the compilers are to be commended for placing this first Georgia list on a solid foundation. There are, however, a few errors in judgment: the record (p. 49) of a Yellow-bellied Flycatcher seen near Atlanta on September 21, 1930, is highly questionable, for in fall plumage the species cannot be distinguished with certainty in the field from some extremely yellow-plumaged individuals of the Acadian Flycatcher (there are even museum specimens of the two species that can be differentiated only with difficulty); sight records (p. 50) of the Least and the Alder Flycatchers in spring are subject to the same criticism.

The authors give the specific records of occurrence for birds that are uncommon in the state, as well as an outline of the local distribution of those species whose occurrence is not statewide. In this connection, however, I would remark that the Chuck-will's-widow is listed (p. 47) as breeding over the entire state though I know of no actual nesting record for extreme northern Georgia.

It is interesting to note that the authors record transient migrants as generally rare or absent in spring in southern Georgia. This shows that the "coastal hiatus" in spring migration extends eastward across the entire coastal region. Likewise of interest is the information that certain warblers that were known to breed in the Alleghenies as far south as North Carolina also breed southward to northern Georgia.

Although the main body of the work is devoted to the annotated check-list and the annotated bibliography of Georgia ornithology, there is, in addition, a list of Georgia ornithological societies and bird clubs; a list of publications devoted exclusively to Georgia birds; an ornithological map of the state with an all too brief discussion of the physiographic regions; and an historical account of Georgia ornithology which gives a brief biographical commentary on a number of naturalists, beginning with Mark Catesby (whom too often we think of only in connection with South Carolina), John Abbot, the Bartrams, the LeContes, and Alexander Gerhardt, but which omits mention of J. J. and J. W. Audubon and of a number of recent field ornithologists who have worked in the state.

The book is well printed although there are a few typographical errors; the system of indenting the second line of the paragraph beginning the account of each species is confusing to the eye; and the annotations in the bibliography might better have been set apart typographically from the titles so that the two could be differentiated at a glance; also the book lacks both an index and the "running heads" which in works of this type usually serve as useful guides to ready reference.—G. H. Lowery, Jr.

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To the Editor of the Wilson Bulletin:

Your readers may be interested to know that satisfactory progress is being made in producing manuscript for future volumes on the Life Histories of North American Birds. The material for four volumes, including all the birds on the A.O.U. Check-List from the jays to the vireos, has been in Washington for a long time, awaiting publication after the war.

Two volumes on the wood warblers are now nearly completed, awaiting a few contributions from others. I am now starting work on the next volume, to include the birds from the weaver finches to the tanagers, and I am taking this opportunity to solicit contributions of notes on habits and photographs relating to birds in the three families, Ploceidae, Icteridae and Thraupidae.

Previous contributions have been very helpful, and I hope they will continue.

Taunton, Massachusetts A. C. BENT

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NEW LIFE MEMBERS

THEODORA NELSON, Assistant Professor of Biology at Hunter College of the City of New York, received her undergraduate training at the University of Wisconsin and then went to the University of Michigan, where she received the Ph.D. degree in 1939. For several years she assisted in the ornithology courses at the University of Michigan Biological Station at Douglas Lake, and, jointly with the late Frank N. Blanchard, prepared an account of the avifauna of the whole Douglas Lake region. She has also completed for publication an extensive report on the life history of the Spotted Sandpiper.

OLIN SEWALL PETTINGILL, JR., Vice-President of the Wilson Ornithological Club, graduated from Bowdoin College in 1930 and later received the Ph.D. degree in ornithology from Cornell University. He is Assistant Professor of Zoology at Carleton College and in summer teaches the ornithology courses at the University of Michigan Biological Station at Douglas Lake. His very productive bird photography expeditions have taken him to many parts of North America, from Hudson Bay south to Florida, Louisiana, and Mexico. In addition to many shorter contributions, he has published an important monograph on the American Woodcock and a laboratory and field manual of ornithology.

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